Diversity of Form, Content, and Function in the Vocal Signals of Adult Male Blue Monkeys (*Cercopithecus mitis stuhlmanni*): An Evolutionary Approach to Understanding a Signal Repertoire

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ABSTRACT

Diversity of Form, Content, and Function in the Vocal Signals of Adult Male Blue Monkeys (*Cercopithecus mitis stuhlmanni*): An Evolutionary Approach to Understanding a Signal Repertoire

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In species across virtually every vertebrate taxonomic division, vocal signals play key roles in predator avoidance, reproduction, competition, and mediating social interactions. Understanding signaling systems, and the various selection factors relating to their evolution and maintenance, therefore provides unique insight into species' behavior, social dynamics, and evolution. Decades of research has greatly improved knowledge of animal signals and how they are used, yet understanding of the mechanisms by which entire communication systems operate and evolve remains incomplete.

The research presented in this dissertation examined the vocal repertoire of adult male blue monkeys (*Cercopithecus mitis stuhlmanni*). Specifically, I examined three elements of vocal signals – acoustic structure, signal content, and adaptive function – across the entire male repertoire, and used results to infer mechanisms of selection on signal usage and divergence. During 12 months of fieldwork in the Kakamega Forest, Kenya, assisted by a team of trained research assistants, I used a combination of natural observation, playback experiments, and digital audio recordings to examine vocal behavior of 32 adult males and responses to their calls by males and 62 adult females from 12 social groups and the surrounding area.

Analyses of digital recordings identified six distinct call types used by adult males: *ant*,

boom, *ka*, *katrain*, *nasal scream*, and *pyow*. The repertoire is best described as discrete, though some gradation occurs between *pyows* and *ants*. To identify signal content – attributes of signalers reliably indicated by features of signals – I investigated each call types' relationship to callers' identity, social status, body size, and attention to external variables (e.g. predators). Results showed that at least three call types (*boom*, *katrain*, *pyow*) were reliable indicators of identity, and features of at least one call type (*pyow*) were correlated with body size. Resident males used all call types whereas "bachelors" used only *nasal screams*, indicating social status is content in all calls except *nasal screams*. Two calls (*ka*, *katrain*) were strongly associated with and essentially exclusive to aerial predators, and *ants* had a similar relationship to terrestrial predators. The *pyow* and *boom* were each associated with multiple external variables, demonstrating that these two calls do not include any specific external stimulus in content. Lastly, the content of *nasal screams*, used exclusively during aggression with other males, included presence of another male.

I tested four separate, non-exclusive functional hypotheses for each call type, using predictions relating to receiver response to hearing calls, as well as variation in temporal, demographic, and contextual patterns of usage. The *ka*, *katrain*, and *ant* each clearly functions in predator avoidance, with the first two relating specifically to aerial predators and the latter specifically to terrestrial threats such as snakes and dogs. Notably, the *katrain* also caused rival males to move away from callers, consistent with a mate defense function. The *pyow*, best described as a general alerting signal, demonstrated a clear role in repelling rival males, yet also functioned in facilitating within-group cohesion. The *boom* showed a clear role in affiliative interactions between callers and

females in their groups, possibly functioning as a signal of benign intent, and was the only call type associated with proceptive interactions and an increase in number of estrous females, indicating a function in mating. Like *pyows* and *katrains*, *booms* also have a secondary function of repelling rival males.

The results of this study provide a comprehensive assessment of the structural and functional diversity of an entire repertoire, as well as insight into the socio-ecological mechanisms by which signal diversity evolves and is maintained. Furthermore, the research presented here demonstrates the importance of a comprehensive approach – one that evaluates form, function, and content of entire repertoires – to understanding the use and evolution of communication systems.

TABLE OF CONTENTS

LIST OF TABLES AND FIGURES

CHAPTER 2

CHAPTER 3

CHAPTER 4

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DEDICATION

To Gabriel, of course

STATEMENT OF ETHICAL STANDARDS

The research presented in this dissertation adhered to the Animal Behavior Society guidelines for the treatment of animals in behavioral research and teaching. Fieldwork protocols were approved by the Columbia University Institutional Animal Care and Use Committee (protocol # AC-AAAC0811). No animals were harmed in the execution of this research.

CHAPTER 1

AN EVOLUTIONARY PERSPECTIVE ON ANIMAL COMMUNICATION AND THE DIVERSIFICATION OF SIGNAL REPERTOIRES.

INTRODUCTION

In virtually every known taxon, communication plays key roles in animals' reproduction, competition, and survival (reviewed in Bradbury & Vehrencamp 1998; Searcy & Nowicki 2005), and the diversity of signals used is indeed staggering. The loquacious brown thrasher (*Toxostoma rufum*), for example, uses more than 2,000 distinct signals (Boughey & Thompson 1981), in contrast to the taciturn toads that generally get by with fewer than five (reviewed in Gerhardt 1994). The vocal rumbles of African elephants (*Loxdonta africana*) rarely go above 15 hertz (Poole et al. 1988), rendering them as inaudible to human listeners as the 20,000 Hz contact calls of some microchiropteran bats (e.g. Monroy et al. 2011); for perspective, consider that adult humans speak in the range of 110-220 Hz.

Since Aristotle's *Historia Animalium* in the 4th century BCE, scientists have been keenly interested in the sounds, scents, and displays exhibited by animals, acknowledging the obvious relevance of these behavioral elements to understanding species' ecology and sociality. Today, an enormous amount of research continues to improve our understanding of how animals use and perceive individual signals (reviewed in Hauser 1996; Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003), yet understanding of how entire signal systems evolve remains incomplete. What explains the diversity of signals used, and the extreme variation even among closely related species? What

selection factors drive divergence among signals, transforming, for example, a presumptive ancestral utterance into a full repertoire of distinctive vocal signals?

This chapter presents a framework for examining signals, and vocal signals in particular, from an evolutionary perspective. It begins (section 1) by reviewing principal definitions of communication and some of the key concepts related to selection on signals and signal systems, including theoretical perspectives on how the reliability (i.e. *honesty*) of signals is achieved and maintained. (2) Focusing on one particularly important communication modality among vertebrates, this review then discusses vocal signals, including the physiology of production and its relationship to acoustic characteristics of signals. (3) Using vocal signals as an example modality, I then explore how different selection factors could lead to signal divergence and the expansion of species' repertoires. (4) Lastly, this chapter outlines a comprehensive approach to examining signals – one that evaluates structure, content, and function in the context of entire repertoires – to illustrate the benefits of examining communication through a behavioral ecology lens. Throughout this discussion, examples are drawn primarily from one class of vocal signals, the so-called *loud calls* used by a variety of amphibians, birds, and mammals.

1. Communication and Evolved Signals

Given the central importance of communication to understanding animals' behavior, ecology, and evolution, the considerable disagreement and confusion regarding what communication actually *is* can be somewhat disquieting. Examining the substantial literature devoted to animal communication reveals various and sometimes conflicting

definitions, as well as assorted metaphors, similes, and shorthand (Mellor 1990; Hauser 1996; Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003). Despite various explicit and implicit differences regarding its constituent elements, however, there appears to be wide agreement that communication, fundamentally, involves transmission of information from a signaler to a receiver (Hauser 1996). For example, in what is generally considered a foundational text in animal communication studies, Bradbury and Vehrencamp's (1998, pg. 354) definition emphasizes that communication is the "provision of information that can be utilized by a receiver to make a decision." This definition, and those that similarly emphasize the importance of information transmitted and received, provides an intuitively logical, criterion-based approach to examining behavior; it is however, intrinsically mechanistic, and as such its application to examining evolutionary processes is limited.

Early theoretical examinations of the evolution of communicative signals evolve focused primarily on the adaptive interests of signalers only. Given that selection favors actions that benefit the actor, it follows that signals are selected because they alter receivers' behavior in ways that benefit the signaler (Wilson 1975; Dawkins & Krebs 1978). This perspective provides a more evolutionary-based definition of communication as occurring "when the action of or cue given by one organism is perceived by and thus alters the probability pattern of behavior in another organism in a fashion adaptive to either one or both of the participants" (Wilson 1975, p. 111). Because this manipulation paradigm, however, tends to underestimate the importance of potential costs or benefits to receivers, Wiley (1983) and Krebs and Dawkins (1984) noted that anything less than a net benefit to *both* signaler and receiver would likely see the demise of a signal; receivers

responding to signals in ways that are costly to themselves would be selected against, and signalers should not produce signals unless they evoke beneficial response. This dynamic model for signal evolution requires balancing interests of signalers and receivers, suggesting that selection ultimately favors signals that benefit signalers *because* they have relevance to receivers' fitness priorities (Krebs & Dawkins 1984; Krebs & Davies 1993; Maynard Smith & Harper 2003).

1.1 Reliability and Selection for Honest Signals

Assuming even a minimal cost to responding, signals that are not relevant to receivers should be ignored, and selection should thereby favor signals that are, on balance, reliable indicators (i.e. "honest") of signaler attributes. The question of *how* the reliability of signals is achieved and maintained continues to be a central topic in animal communication (Hauser 1996; Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003; Searcy & Nowicki 2005). Most of the theoretical and empirical attention to signal honesty has focused on contexts in which signaler and receiver have opposing interests (e.g. contestants disputing a resource would each benefit by the other's withdrawal). In such cases, if receivers evolve fixed responses in concurrence with signals that are generally honest, signals that are *not* reliable could easily invade (i.e. "cheating"; e.g. weaker contestants could employ signals that exaggerate their fighting ability) unless there is some mechanism for maintaining honesty (Maynard Smith 1974; Dawkins & Krebs 1978). Even in contexts in which animals have shared fitness interests (e.g. close relatives), however, signal reliability is essential to function.

The following provides a brief summary of the dominant theoretical perspectives on how signal honesty can emerge. Importantly, most of these mechanisms are not exclusive of one another in either principle or application.

1.1.1 Costly Honesty When signalers and receivers hold disparate fitness priorities (e.g. a male benefits by mating with practically any female whereas females should invest in "high quality" males only; Andersson 1994), selection might favor receivers' responding only when a signal's honesty is guaranteed by its costs. The handicap principle (Zahavi 1975, 1977; Grafen 1990), foundational to many examinations of honesty and especially in sexually selected signals, posits that a signal can achieve reliability by being costly to produce, thereby ensuring that only signalers capable of bearing its burden can use it, or do so effectively. Costs can accrue in a variety of ways, most typically characterized in terms of signals' being 1) *inherently costly* (e.g. in some frogs, male courtship vocalizations are among the species' most energetically demanding activities; Taigen & Wells 1985), or relatively costly to produce under privation (e.g. nutritional hardship, Iwasa & Pomiankowski 1991; or parasitic infection, Hamilton & Zuk 1982); 2) *developmentally costly* (e.g. in some songbirds, characteristics of adult song reflect nutritional stress during early development, and thus may indirectly reflect genetic traits associated with resiliency; Nowicki et al. 1998); or 3) *strategically costly* (e.g. signaling can make individuals conspicuous to predators or competitors, and may sacrifice time spent feeding; reviewed in Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003).

The idea of strategic costs enforcing honesty has been expanded to include signals referred to as *conventional* or *badges of status*. For such signals, there may be little inherent or developmental cost associated with production, but producing the signal increases aggressive contests; selection would therefore favor signaling by only those able to defend themselves. For example, in some species in which socially dominant animals exhibit distinctive markings, if subordinate animals are experimentally augmented to resemble dominants, they receive increased aggression (e.g. Harris' sparrows, throat patches, Rohwer 1977; paper wasps, unique facial patterns, Tibbetts & Dale 2004).

1.1.2 Indexical Honesty Some signals, or modular components of signals, are honest by virtue of their intrinsic relationship to the anatomical or physiological traits they indicate, and are referred to as *index cues* (Fitch & Hauser 1995; Vehrencamp 2000; Maynard Smith & Harper 2003). In the vocalizations of most mammals, for example, a negative correlation between a signal's formant dispersion (i.e. distance between frequency resonances) and the signaler's skeletal length derives from intrinsic properties of mammalian skeletal morphology and the physics of sound production (reviewed in Fitch & Hauser 2002). Formant dispersion and other indices (e.g. displays that involve signaler's rising up to full height), therefore, achieve reliability not by cost but because the structure of the signal is constrained by inviolable properties of its production.

1.1.3 Mutual Interests, Shared Benefits As mentioned, examination of signal honesty has generally emphasized cases in which the fitness priorities of signalers and receivers

are in conflict. Such an antagonistic perspective suggests a need for strong mechanisms for maintaining honesty. Animals regularly use signals, however, in contexts where the interests of signaler and receiver are relatively aligned, and, though there may be little benefit to "cheating," reliability is still fundamental to signal function.

Where a common benefit to both signaler and receiver is inherent in the signal context (e.g. in a predator event if signaler's kin are vulnerable), honesty may be maintained by relatively simple mechanisms (reviewed in Maynard Smith & Harper 2003). The simplest models propose that reliable signals thrive when there is sufficient selection against unreliable signals (Viljugrein 1997), resulting in honesty by attrition, or when receiver response is frequency dependant (e.g. Dawkins & Guilford 1991) such that the more a signal is used reliably (e.g. "alarm" calls given when predator is actually present) the more selection will favor consistent receiver responses. So-called "reputation signals" are similarly frequency dependant, with honesty sustained when repeated interactions and memory of past encounters results in receivers being less likely to respond to known cheaters (van Rhijn & Vodogel 1980); such a mechanism could relate to *signals of benign* intent in highly social species (e.g. having recently attacked a group mate, a baboon may approach her victim after aggression subsides; producing soft grunts while approaching increases likelihood of a peaceful interaction; Silk et al. 1996; Cheney & Seyfarth 1997).

1.1.4 All of the Above Because reductionist classification is tremendously practical in generating and testing hypotheses, researchers sometimes overlook that it is fundamentally heuristic. Partitioning explanations according to distinct mechanisms can potentially mischaracterize selection as unidimensional, though the reliability of any

signal is likely to be influenced by multiple factors. Crows by domestic roosters, for example, are conspicuous vocal signals that invite attacks by other males and thus fit the *badge of status* criteria (Leonard & Horn 1995); however, acoustic features of crows covary with testosterone levels (Furlow et al. 1998), suggesting the signal may constitute an index of condition or aggressive tendencies; and, because high levels of testosterone have an immunosuppressive effect (Peters 2000), such calls might also, indirectly, relate to a handicap. Furthermore, characterizing signalers and receivers as having opposing interests may, in some cases, be a matter of perspective; in aggressive encounters, for example, though greater significance is often attributed to the disparate interests of combatants, both benefit by avoiding escalation of aggression (Maynard Smith & Harper 2003).

2. VOCAL SIGNALS

The importance of vocalizations in mediating relationships among animals is well demonstrated in a wide variety of vertebrate taxa (reviewed in Todt et al. 1988; Catchpole & Slater 1995; Bradbury & Vehrencamp 1998; Gerhardt & Huber 2002; Maynard Smith & Harper 2003). In species occupying diverse habitat types, social systems, and ecological niches, vocal signals play essential roles in agonistic and affiliative encounters, predator avoidance, territorial disputes, and all manner of reproductive interactions. The convergence on vocal communication across Amphibia, Aves, and Mammalia likely reflects advantages acoustic signals have relative to other modalities (i.e. visual, chemical, tactile, electrical). For example, vocal signals can vary

in multiple dimensions (e.g. duration, amplitude, frequency), and thus provide a high degree of functional flexibility. They can be activated, terminated, or changed rapidly, accommodating the variability of socially or ecologically volatile environments. Perhaps most importantly, some vocal signals have the potential to travel over great distances and through or around objects, and are thus especially useful for animals occupying visually obstructed habitats (e.g. forest-dwelling primates) or maintaining social ties among dispersed conspecifics (e.g. elephants, whales).

2.1 Signal Production

Vocalization is the production and modification of sound using the lungs, vocal structures (e.g. larynx, in mammals, syrinx, in birds), and the various muscles, cavities, and sinuses associated with the pharynx and craniofacial anatomy. A species' vocal repertoire, as with any suite of related characters, is therefore constrained by this underlying morphology and the ability to manipulate it. While patterns of use and adaptive functions of signals may be examined in a strictly behavioral context, thorough study of vocal communication should take into account the physiological mechanisms that are involved in the production of these signals (Fitch & Hauser 1995, 2002).

Examination of vocalizations often draws on *source-filter theory* (Müller 1848; Fant 1960) as a model for the relationship between signals' acoustic structure and the anatomy of production; though formulated to examine variation in human vocalization, source-filter remains the dominant theoretical perspective in studies of most vertebrate vocal systems. Summarized, source-filter theory posits that acoustic structure of a vocal signal reflects a sound generated by a particular source having been modified by the application

of frequency filters. In mammals, the source sound is vibration of the vocal folds resulting from air being forced through the larynx by the lungs; the tension of the vocal folds relative to the air pressure sets the frequency of this initial sound, the vocalization's fundamental frequency (F0) or pitch. As this sound moves up through the tubular supralaryngeal vocal tract, some frequencies are selectively amplified (resonances) while others are dampened or filtered out. As the filtered sound continues toward the exit, it is further modified by movements and morphology of the pharynx, craniofacial sinuses, oral cavity, tongue, and lips, accentuating or diminishing energy in particular frequencies and shaping the final signal (detailed in Fitch & Hauser 1995, 2002).

2.1.1 Specialized Anatomy In mammals, the larynx is considered "vocal" anatomy and the mucosae occluding its opening are referred to as "vocal" folds. Like other elements of the supralaryngeal morphology, however, these features evolved with roles in ingestion, breathing, and protecting the airway, and vocal behavior remains constrained by these primary functions. In some species, constraints are relaxed somewhat by specialized structures that function to augment vocalizations; the evolution of these traits underscores the importance of vocal communication in many species. For example, in many anurans some of the air expelled during vocalization flows into a submandibular sac that inflates to impressive proportions before returning air to the lungs for use in subsequent calls (Gans 1973; Dudley & Rand 1991); as Fitch and Hauser (2002) point out, this can serve two functions – rate of calling can increase beyond the limits of lung capacity and the inflated air sac may act in impedance-matching, essentially amplifying the signal by increasing the efficiency with which sound energy is conducted from

anatomy to atmosphere. In African elephants and southern elephant seals, the proboscis functionally elongates the vocal tract beyond the constraints of the caller's neck and head and allows modification of acoustic structure (Soltis et al. 2009; Sanvito et al. 2007). The syrinx in birds is perhaps the most extreme morphological adaptation relating to vocal behavior, and its decoupling of vocalization from protecting the airway has likely played an important role in the diversification of song types across the avian order (Catchpole & Slater 1995; Fitch & Hauser 2002).

In primates, a classic example of anatomical adaptation for vocalization is in *Alouatta spp*., the aptly named howler monkeys. Adults of both sexes amplify vocalizations with a hollow hyoid bone that, proportionally, is massive compared to that of other primates; for perspective, consider that an adult male Guinea baboon, at ~20kg, is easily twice as large as an adult male mantled howler, at ~7 kg (Groves 2005), yet the hyoid of the howler is nearly twice that of the baboon (3.2 cm versus 1.64 cm; Hilloowala 1975). In several New World monkey genera, larynges are enlarged and the hyoid and thyroid cartilages are expanded and dilated in both sexes (e.g. *Aotus*, *Callicebus*, *Pithecia*; Dixson 1998). The increased size of the larynx allows lower fundamental frequencies, and expansion of the hyoid and thyroid cartilages increase resonances, suggesting possible selection in relation to advertising body size (Fitch & Hauser 2002).

Laryngeal air sacs, pouch-like extensions from the larynx or other parts of the supralaryngeal vocal tract, are found in many primate genera, and phylogenetic reconstruction suggests their presence is ancestral in catarrhines and possibly even all haplorrhines (Hewitt et al. 2002). Despite their prevalence, they have been well-studied in only a few groups – notably *Alouatta spp*., *Cercopithecus spp*., and apes (Gautier

1971; Fitch & Hauser 1995; Dixson 1998; Hewitt et al. 2002) – and little research has empirically examined their performance, though some role in either respiration, vocalization, or both has been suggested for most taxa in which they appear. Air sacs unquestionably modify vocal signals, though the exact mechanisms by which they do are uncertain. Air sacs likely function in impedance matching (as described for frogs, above) and hence act to amplify calls (Fitch & Hauser 2002), a hypothesis supported by Gautier's (1971) demonstration that puncturing the air sac of a Debrazza's monkey (*Cercopithecus neglectus*) did not alter acoustic structure of its *boom* call but nearly extinguished amplitude. Because air sacs can be variably inflated, Fitch and Hauser (1995) suggest they may also act as "tunable resonators," changing the vocal resonance and hence lowering pitch and formant frequencies (e.g. *Colobus guereza*, Harris et al. 2006). Air sacs may also supplement lung capacity, acting as reservoirs that allow calling rate and call duration to surpass limits of lung volume (Schön-Ybarra 1995), or allowing re-breathing during long or strenuous vocalizations (Hewitt et al. 2002).

3. Divergence of Signals

Earlier, I discussed various mechanisms by which individual signals are maintained by selection. Examining signals as singular, fixed entities provides a point from which to explain why each persists, yet does little to explain how signals actually come about. Unlike human language, in which neologisms may enlarge vocabulary *ex nihilo*, species' signal repertoires are unlikely to expand by the sudden appearance of newly formed signals. Instead, like any other heritable trait, new signals likely diverge from other

signals or behaviors, and reflect long evolutionary histories and the cumulative influence of numerous selection factors. The diversity of signals across taxa, and the extreme variation even among closely related species, questions the utility of any one model of how signal systems evolve; theoretical and empirical research, however, provide a strong foundation for inferring diversification of vocal repertoires.

Animal signals are hypothesized to originate from behavior with no communicative function. Under the selection processes described earlier, a behavior capitalizing on observers' pre-existing innate responses (i.e. sensory bias) could become increasingly stereotyped, or *ritualized*, until eventually *emancipated* from its behavioral origin to function in communication (Tinbergen 1952; Morris 1956; Lorenz 1970; Wiley 1983; Johnstone 1997). For example, the bared teeth yawn, an aggressive signal in many primates (reviewed in Vick & Paukner 2010), possibly originated as a reflexive, physiological response to increased arousal (i.e. displacement activity) during encounters between competitors and, because exposed canines may indicate fighting ability, over time became fixed as a communicative signal.

Because the larynx' roles in respiration and protecting the trachea during swallowing undoubtedly preceded its role in vocalization, a reasonable assumption is that vocal signals derived from sounds associated with breathing. This suggests a cough-like sound as the likely origin of vocalization as a signal modality, yet does not explain the diversity of signals; it is implausible that each vocal signal in a species' repertoire was individually emancipated from non-communicative respiratory action. A more parsimonious explanation is that disruptive selection acting on variation within existing signals creates new signals (i.e. divergence rather than emergence) and drives expansion of repertoires.

3.1 Modeling Signal Divergence

Charles Darwin, with characteristic prescience, provided an evolutionary basis for distinctiveness of signals in animals' repertoires. Noting that "opposite" emotional states (e.g. angry versus affectionate) provoked an "involuntary tendency to the performance of movements of a directly opposite nature," Darwin (1872) proposed that some behavior acts on the 'principle of antithesis.' A domestic cat, for example, raises its tail and arches its back during affinitive interactions, and flattens out during aggression. If selection favors responding based on the arousal state of others (e.g. flee if aggression is imminent), it could also favor signalers that provide reliable indicators of their different arousal states; a relationship between arousal state and signal structure thus provides an elegant evolutionary explanation for distinctive signal types.

A mere century after Darwin's assessment, researchers seeking to explain patterns of structural variation in signals again addressed signalers' arousal state. Evidence from across mammals and birds that vocal signals associated with similar social and ecological contexts tend to share certain acoustic characteristics led to the idea that vocal signals conform to *motivation-structural rules* (Morton 1977); in summary, vocalizations used in aggressive contexts are more loud, harsh (i.e. energy diffused across frequencies), and low frequency, whereas those used in affiliative or appeasement contexts are more quiet, tonal, and high frequency (reviewed in Owings & Morton 1998). These structural differences undoubtedly reflect changes in vocal production resulting from physiological changes associated with arousal (e.g. fear is accompanied by increased respiration and muscle tension in humans; Ax 1953). In our hypothesized ancestral cough example, acoustic variation reflecting physiological correlates of arousal could thus allow

divergence into, perhaps, a louder, harsher variant during high arousal and a softer, more tonal variant reflecting more relaxed states.

The concept of motivation-structural rules described by Morton (1977, 1982) provides an excellent model to explain the divergence of signals within repertoires based on differences in signaler arousal. The tendency toward dichotomous examples (e.g. aggressive *vs.* affiliative signal contexts), however, leaves questions when trying to explain the existence of multiple signals *within* the same functional class. For example, many species have multiple distinct call types used during different predator events. In some cases, this is explained by differences in response urgency (i.e. relative perceived threat based on distance and speed of predator; Robinson 1981; reviewed in Furrer & Manser 2009) and thus still consistent with variation in signaler arousal. The observation that some signals may be indicators of specific *types* of stimuli, not urgency, however, indicates that animal signals might be more complicated than previously thought. For example, classic research by Struhsaker (1967) and Seyfarth et al. (1980) showed that vervet monkeys have acoustically distinct calls that correspond with different predator types (i.e. eagle, leopard, and snake alarm calls) and that receivers respond to calls as if the particular predator were present. In other mammals and birds, similar observations of distinct signals used with comparable but categorically distinct stimuli (reviewed in Marler et al. 1992; Macedonia & Evans 1993; Evans & Marler, 1995; Hauser 1996; Bradbury & Vehrencamp 1998; Blumstein 1999; Maynard Smith & Harper 2003; Seyfarth & Cheney 2003a; Searcy & Nowicki 2005) have added a new dimension to animal communication research and introduced the idea of referential communication.

Studies of animal communication conventionally draw clear distinctions between signals that are essentially affective (i.e. relate to the emotional, arousal, or motivational state of the signaler) and those that are referential or semantic (i.e. relate to specific phenomena *external* to the signaler) (Macedonia & Evans 1993). Debate over the applicability of these categories remains an exceptionally generative research topic, though much of the focus is on mechanistic explanations relating to how signalers and receivers process signals; from an evolutionary perspective, referential alarm calls are generally thought to arise in species when the presence of predators with different hunting strategies (e.g. aerial vs. terrestrial) leads to adopting multiple methods of escape (Marler 1977; Cheney & Seyfarth 1990; Macedonia & Evans 1993). The common assertion that referential signals, because of their specificity of stimulus, are distinguished from affective signals (Macedonia & Evans 1993), however, suggests that referential signals do not fit the arousal based model of divergence described above because arousal associated with, for example, three different alarm calls is presumably quite similar (Seyfarth & Cheney 2003a). I see no reason, however, that selection acting in consort with the principles of motivation-structural rules could not explain the occurrence of distinct signals associated with different but categorically similar stimuli (e.g. aerial and terrestrial predators). As illustration, imagine a hypothetical species having evolved a single call type that is used in a variety of disturbance contexts (e.g. aerial predators, terrestrial predators, aggressive encounters). It is quite likely that the signaler's arousal state would vary, perhaps subtly, among the different stimuli and thus, though only one signal *type*, there would undoubtedly be some acoustic variation; if the relationships between stimulus (e.g. predator class), arousal, and acoustic variation were even

moderately consistent, it could suggest incipient divergence of signal types. If receivers benefit sufficiently from having different responses (e.g. different strategies depending on whether predator is aerial or terrestrial), selection should favor categorical perception of the acoustic variation (Harnad 1987; Maurus et al. 1988; Seyfarth & Cheney 2003b) as well as signalers amplifying that variation, until distinct signal types emerged. Seyfarth and Cheney (2003a) argue that such a model is particularly unlikely, as it might suggest that "over evolutionary time, natural selection has acted in such a way that all [signalers] now "agree" on precisely what level of excitement (or fear) is associated with each type of predator." This argument, however, misrepresents the process of selection described; selection would not require all signalers having identical arousal responses, only that they evolve the ability to sufficiently distinguish among stimuli (via innate recognition, selective habituation, or learning; Tinbergen & Lorenz, reviewed in Schleidt et al. 2011) and have categorically different responses to different stimuli.

4. Examining Vocal Signals: A Comprehensive Approach

The model outlined above illustrates how selection favoring distinctiveness, coupled with even minor variation in signal production could allow entire repertoires to arise and expand. Though rooted in evolutionary principles and supported by empirical and theoretical research, it is, like all models, a simplification and is not suggested as an encompassing explanation of the processes by which signals diverge. Repertoires, from frogs to birds to elephants, are extremely varied and each reflects the unique evolutionary trajectories of the species and specific ecological and social contexts to which it belongs.

The view of signals as derived traits sharing an evolutionary history, however, provides a framework for thorough investigation of the adaptive significance of signal features; whether examining functional hypotheses, content, or the influence of various social, ecological, or phylogenetic factors, communication research benefits by acknowledging, and addressing, the historical and evolutionary relationships among signals.

Communication research conventionally partitions animal vocal behavior, frequently investigating and presenting individual signals or components thereof (e.g. fundamental frequency) as discrete entities. The relatedness of signals within repertoires suggests, however, that examining single components or subsets of signals would constrain the inferential power of studies, and that a comprehensive approach is likely to provide greater insight into how animals communicate. Such an approach poses considerable challenges, both in the execution and presentation of research, but the results of comprehensive examinations greatly enhance opportunities for comparative studies that can expand understanding of communication within and among taxa.

The following section briefly summarizes three elements essential to investigations of vocal signals – form, content, and function – and emphasizes the importance of examining signals within the context of entire repertoires. Examples are chosen from several taxa, yet, because vocal behavior of adult male blue monkeys (*Cercopithecus mitis*) is the subject of the subsequent chapters, many will relate to primates and especially to the conspicuous vocal signals known as *loud calls*.

4.1 Form

The form of any signal can be described in terms of its constituent parts and also as a whole. Researchers might, for example, quantify the duration, span, and angle of a flamingo wing salute, and also examine variation in the display's rate of usage within and among individuals and populations. Examining the structure of vocal signals is no different in principle, though evaluating features of acoustic entities poses certain challenges. Relying on observers' inherently subjective perception of a vocalization is limiting, to say the least. However, technological advances over the past several decades have allowed for more objective approaches – spectrographic analysis enables measurement of structural elements in numeric terms and today is one of the most widely applied tools in studies of vocal behavior.

Sound is energy (pressure) moving through a medium (e.g. air, water), typically as longitudinal waves of varying frequencies. Given these attributes, sound can be considered in three dimensions – spectral (frequency), energetic (amplitude), and temporal (duration) – and can be visualized as a spectrogram based on quantified values of these parameters. A variety of computer programs are available, with most using the short-time Fourier transform (STFT), an algorithmic procedure that involves dividing audio data into discrete time samples and calculating the energy at each frequency spectrum. Aligning these discrete samples linearly describes the temporal component while the rendered frequency-energy measures complete the picture: a graphical representation of sound in three dimensions. The resulting spectrogram (and associated power-time oscillograms and power-frequency spectra) allows quantitative assessment of various acoustic features, providing parameters for comparative and descriptive analysis.

Quantitative analysis of acoustic structure is foundational to most examinations of vocal signals. Identifying relationships between various spectral and temporal features of signals and characteristics of signalers, receivers, contexts of use, and habitats is the key means for testing hypotheses relating to signal function and ecological adaptations. Though distinctions at higher levels (e.g. call type) can be extremely useful in examining differences within and among repertoires (akin to macroevolutionary studies), quantifying structural elements provides better resolution and a greater understanding of how acoustic variation may relate to key aspects of species and their social and ecological environments. Furthermore, because the model for signal evolution discussed above predicts that signals exhibiting the most structural similarity are likely the most recently diverged, thorough structural analysis may provide a first step in inferring patterns of divergence.

4.2 Content

Though there are numerous possible mechanisms by which a signal may evoke receiver responses (e.g. by stimulating reflexive neurological responses or by facilitating more complex cognitive processing), evolutionary considerations remain the same: for selection to favor receivers responding in a consistent fashion, a signal must relate to something relevant to the fitness of receivers. Here, I use the term *signal content* to refer, specifically and unambiguously, to attributes of signalers that are associated with signal features in such a way that the signal can be a reliable indicator of the attributes. Signaler attributes may include intrinsic (e.g. species, age, sex, size), extrinsic (e.g. attention to a predator), or even behaviorally flexible features (e.g. likelihood of attacking after

producing signal). Signal features may include visual, chemical, or acoustic characteristics (e.g. color, amplitude) and patterns of use. Signal content (though often termed *information*) has been examined in the vocal signals of several primate species; the following describes the elements of content that are most frequently identified.

4.2.1 Species is reliably indicated in the loud calls of most primates (reviewed in Macedonia & Taylor 1985; Oates et al. 2000; Gautier 1988; Zimmermann 1995; Hohmann & Fruth, 1995). The consistent distinctiveness among species and even subspecies (e.g. ruffed lemur, Macedonia & Taylor 1985) provides a basis for conspecific communication, especially over long distances, and suggests changes in acoustic features of loud calls relate, causally or consequently, to genetic isolation. Research, primarily in birds, indicates that divergence in signals associated with mating may be a first step in speciation (reviewed in Coyne & Orr 2004).

4.2.2 Age-sex class In most anuran, bird, and mammal species, only adult males exhibit loud calls (Searcy & Andersson 1986; Andersson 1994; Searcy & Nowicki 2005). In most primate species, loud calls are similarly biased (Dixson 1998; Wich & Nunn 2002), making their emission a de facto advertisement of age and sex. Being reliable indicators of age and sex may relate primarily to the relationship between some acoustic features (e.g. duration, amplitude, fundamental frequency, formant dispersion) and body size, as larger individuals (i.e. adult males, in many species) are likely to have larger vocal folds, longer vocal tracts, and greater lung capacity. There are some species in which both sexes emit loud calls, yet pronounced sexual dimorphism in acoustic

structure, possibly relating to differences in specialized vocal structures (e.g. air sacs), still provides a reliable indicator of sex (e.g. *Hylobates spp*., Cowlishaw 1992; *Alouatta spp*., Dixson 1998).

4.2.3 Body Size In some taxa, the fundamental frequency (F0) of vocal signals is a reliable indicator of body size (e.g. in most anuran species; reviewed in Gerhardt & Huber 2002), but not in mammals. Formants (i.e. frequency peaks, seen as dark bands in spectrograms; see Chapter 2) reflect resonance frequencies of the signaler's vocal tract; the distance between formants (i.e. dispersion) is negatively correlated with the length of the vocal tract (Fant 1960; Lieberman & Blumstein 1988; Fitch 1997). In most mammals, skeletal length is strongly tied to length of the laryngeal tract (reviewed in Fitch & Hauser 2002), making formant dispersion a reliable indicator of size in several primates and other mammal species (Fitch 1997; Riede & Fitch 1999; Reby & McComb 2003; Harris et al. 2006; Ghazanfar et al. 2007; Sanvito et al. 2007; Vannoni & McElligott 2008).

4.2.4 Condition and Social Dominance The term 'condition' is used both casually and formally in scientific literature, yet as an attribute of individuals is often vaguely defined. Condition relates to some particular or cumulative aspect of energetics, strength, endurance, or immune response, yet how it is measured varies. In studies of free-ranging primates, it can be extremely difficult to obtain more than qualitative metrics for physiological attributes, and researchers often rely on indirect inference. Steenbeek et al. (1999), for example, examining loud calls by male Thomas's langurs (*Presbytis thomasi*),

measured a male's strength as the number of aggressive encounters instigated and success in defending females in his group from other males; this measure covaried with how often males called, suggesting that call rate is a reliable indicator of fighting ability.

In some species, features of calls covary with social dominance or territory ownership. Call usage patterns may reliably indicate dominance rank in chimpanzees (*P. troglodytes*), for example, where higher ranking animals *pant-hoot* more often (Mitani & Nishida 1993), and acoustic features may also vary with rank (e.g. male baboon *wahoo* duration is positively correlated with social rank; Kitchen et al. 2003). Importantly, dominance is not an attribute of an individual, but rather is the agonistic asymmetry *between* individuals (Rowell 1974); when signal features correlate with rank, therefore, it may be more accurate that signal content includes particular (though perhaps unidentified) attributes associated with agonistic success (e.g. size, coalition partners) for which rank may be a cumulative proxy.

Indirect or proxy measures for attributes associated with physical condition are appropriate in many cases, but care should be taken to avoid circular arguments when assessing call features as reliable indicators; without linking signal features to specific relevant attributes (e.g. muscle mass, c-peptides) it is difficult to determine whether vocal behavior *reflects* resource holding potential (RHP) or *influences* it.

4.2.5 Identity That some vocal signals are individually distinctive has been found in a wide range of primate species (e.g. *Pan troglodytes*, Mitani et al. 1996; *Cercopithecus mitis*, Butynski et al. 1992; *Callithrix jacchus,* Goedeking & Newman 1987; *Saguinus oedipus*, Snowdon et al. 1983; *Lemur catta*; Macedonia 1986 *Ateles geoffroyi*; Chapman

& Weary 1990; *Presbytis thomasi*; Steenbeek & Assink 1998; *Pongo spp.*, Delgado 2007). In fact, evidence is so pervasive that researchers often tacitly assume primate vocalizations indicate identity, even in species for which it has not been empirically tested (Tibbetts & Dale 2007); the ubiquity of individual vocal signatures has not been established, however, and caution is always advised. In putty-nosed monkeys (*Cercopithecus nictitans*), for example, one of the male loud calls (*pyow*) is acoustically distinct among individuals while another (*hack*) is not (Price et al. 2008).

4.2.6 External Referents, Context, and Behavioral Commitment As discussed earlier, some animal signals are associated with external objects with such consistency that they are reliable indicators of those objects. Distinguishing intrinsic attributes (i.e. physical, physiological, or social characteristics) from content elements that are "external" may be somewhat heuristic (e.g. my saying, "There's an octopus behind you," refers to an external object, yet still indicates *my attention to* said cephalopod, and thus an intrinsic feature); the distinction is, however, both conventional and convenient for exploring signals. When identifying external objects (e.g. predator types, food items) as signal content, it is critical to examine not only the association between variation in signal features and a particular stimulus, but also the degree to which the association is more or less *exclusive* (Seyfarth & Cheney 2003b). A call type given in association with eagles only, for example, can be a reliable indicator of eagles; a call type given in association with eagles, leopards, and snakes is a reliable indicator of predators, in general; a call type given in association with 'unrelated' contexts (e.g. predators, conspecific aggression, group movement, *and* dawn choruses) cannot include any particular stimulus as content.

The most commonly identified external content variables identified in animal signals are specific types or classes of predators (discussed above). Some species also have vocal signals that are reliable indicators of food (e.g. chickens, Evans & Evans 1999; ravens, Bugnyar et al. 2001; capuchin monkeys, Di Bitetti 2003).

Some vocal signals are linked to signalers' likely behavior after signaling, and thus content can include intention or behavioral commitment. In many birds, for example, song features are related to the signaler's willingness to escalate aggression (reviewed in Searcy & Beecher 2009), and in some primates vocal signals associated with a reduced likelihood of aggression (e.g. during affiliative approach) may indicate the signaler's 'benign intent' (reviewed in Silk 2002). Many primate species also use certain call types consistently before beginning to travel (reviewed in Boinski 2000).

4.3 Function

The function of a behavior explains its reproductive or survival value in terms of the benefit the actor receives (Tinbergen 1963). Though *vocalizing* may have inherent benefits (e.g. in humans, laughing increases immunoglobin levels; Lambert & Lambert 1995), the function of a vocal *signal* is the benefit derived from the response by receivers (though Bradbury & Vehrencamp, 1998, and others follow Smith, 1977, in using function to describe the benefits to *both* signaler and receiver, and thus, essentially, its ability to broadcast particular content).

Identifying function is critical to understanding signals, yet can be exceptionally difficult in cases where there is a substantial lag between signal production and receiver response or the benefit to signalers is otherwise unclear. Not surprisingly, signals used in

predator and aggressive contexts often provide the most conclusive evidence of function, as receiver response tends to be immediate, conspicuous, and unambiguous (reviewed in Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003; Searcy & Nowicki 2005). Signals that function in mate attraction, territorial defense, or maintaining social cohesion often do so in more subtle ways, and the benefit signalers receive may relate more to cumulative rather than discrete receiver responses (Snowdon 2004).

To identify signal function, researchers rely on a number of methods for directly measuring or inferring receiver response. Natural observation, with a large enough sample, can provide direct evidence of receiver response to signals, as well as data for inferential assessment based on contextual, spatial, and temporal patterns of usage (e.g. signals used during predator events are likely to function in predator avoidance; increase in a signal's usage during the mating season may relate to mate attraction, defense, or both). Playback experiments, in which vocal signals are broadcast to receivers, can supplement natural observation while controlling against potentially confounding variables (e.g. presence of predators) that may also affect receiver response. Finally, some functional inferences can be made based on signal structure (e.g. vocal signals with an audible range of hundreds of meters may evoke responses by far away receivers), though conclusions based on structure without other supporting evidence are speculative.

Across taxa, numerous functions have been proposed to explain the roles of vocal signals in predator avoidance, territoriality, social cohesion, affiliation, aggression, and other correlates of survival and reproductive success. Not surprisingly, functional variation described across taxa tends to relate to degree of social complexity; the vocal repertoires of anuran species, for example, are restricted to usually no more than five

calls functioning almost exclusively in reproductive contexts (reviewed in Gerhardt & Huber 2002; Kelley 2004). In contrast, the vocal repertoire of elephants is extensive (Poole et al. 1988), suggesting high functional diversity reflecting the species' complex social dynamics (e.g. regularly interacting family units and strong inter-individual relationships; Moss & Poole 1983).

For many practical reasons, function is better understood for species' more conspicuous vocal signals (e.g. loud calls, song), with functional explanations typically falling into one or more of three general categories – spacing, mate attraction and defense, and predator avoidance. It is important to bear in mind that one signal may evoke different responses from different receivers and thus achieve multiple functions (e.g. females may approach a signaler that males may avoid), and that a single response by receivers may confer multiple benefits (e.g. a 'rallying call' that gathers conspecifics decreases likelihood of predation, increases likelihood of mating, and improves competitive odds against other groups; thus one type of receiver response may achieve functions relating to mate attraction, predator avoidance, and intergroup agonism).

4.3.1 Spacing In most species, maintaining proximity to or distance from particular conspecifics is fundamental to competition over resources and reproductive success, and is the foundation for virtually all social dynamics. Vocal signals that function to regulate space between a signaler and conspecifics do so by evoking or inhibiting phonotaxis in receivers (i.e. calls may attract, repel, or cause receivers to cease moving).

For group living animals, signals are conventionally divided according to within-group or between-group spacing functions (note: though not technically different, inter-

male spacing functions are discussed with mate defense, below). Where there are benefits from sustained proximity to group mates (e.g. predator avoidance, food discovery, competition between groups), vocal signals in many species function to maintain group cohesion; these typically operate as *rallying calls* that initiate travel by group members toward or with the signaler, or *contact calls* that allow dispersed group mates to monitor locations of others (reviewed for primates in da Cahuna & Byrne 2009). In African elephants (*Loxodonta africana*), extremely low frequency vocal 'rumbles' are perceptible as far as 10 km (though individually identifiable only up to 2 km), and some have been shown to facilitate coordinated movement by dispersed members of kin groups (Poole et al. 1988; Larom et al. 1997; McComb et al. 2003; Soltis et al. 2005; Leighty et al. 2008). The songs of some mysticetes species (baleen whales) are similarly low-frequency and, under certain conditions, can potentially transmit over hundreds of kilometers (Payne & Webb 1971); although seasonal and diel patterns of vocal behavior provide logical inferences that these songs function to coordinate travel associated with breeding and feeding (e.g. Clark & Clapham 2004; Oleson et al. 2007), it is exceptionally difficult to test function of whale songs empirically.

Regulating space between groups is another, and perhaps concurrent, function hypothesized for some vocal signals, and by far the most commonly offered for primate loud calls. Signals may repel other groups in an immediate sense or by 'acoustically marking' a territory or other defended site (Waser 1975a). In several species, loud calls may function as *advertisements of occupancy*, similar to territorial scent markings. Some howler monkeys (*Alouatta spp.*), for example, call "spontaneously" throughout their home range, and call more in response to other groups perceived within their home range

and less to groups outside their home range (Sekulic 1982; da Cuhna & Byrne 2006); similar observations suggest a territorial function for wolf howls (Harrington & Mech 1979, 1983). Non-territorial species may also use loud calls to regulate inter-group space by encouraging mutual avoidance (e.g. gray-cheeked mangabeys, *Lophocebus albigena*, base group movement in relation to other groups' *whoop gobbles*; Waser 1975b).

4.3.2 Mate attraction and defense "The songs of passerine birds have two main functions: to repel rival males from their territory and to attract and stimulate females to breed with the male" (Catchpole, 1989). Though Kroodsma and Byers (1991) rightfully caution against such a generalization given that these functions, especially attraction of females, are often concluded from indirect evidence, there is little doubt that vocal signals play important roles in mate attraction and defense in many taxa (reviewed in Andersson 1994).

There is considerable direct evidence that vocal signals function in both inter-male spacing and mate attraction in many anurans. In most frogs, for example, loud calls occur almost exclusively in reproductive contexts, females preferentially approach males based on their calls, and males advance into or retreat from mating areas based on the calls of competitors (reviewed in Gerhardt & Huber 2002; Kelley 2004). Bird song is similarly linked to functions of attracting mates and repelling rivals, with the most conclusive evidence relating to song as a territorial display; in several species, for example, both observation and speaker-replacement experiments have demonstrated that producing songs reduces intrusion by other males (reviewed in Searcy & Andersson 1986; Catchpole & Slater 1995).

Similar functions are clearly associated with vocalizations in mammals, though research has proceeded more slowly (reviewed in Clutton-Brock & McAuliffe 2009). Some of the most compelling work has focused on the roars of male deer, with evidence suggesting these calls are functionally analogous to the territorial calls of birds and frogs. In red deer (*Cervus elephas*), for example, males exchange roars during the mating season and younger, subordinate males typically retreat from roars by larger males (Clutton-Brock & Albon 1979), while females preferentially approach roars (and playbacks) of larger males (Charlton et al. 2007); perhaps the most persuasive evidence of a direct role in mate attraction is that exposure to male roars accelerates female ovulation (McComb 1987).

In primates, a mate attraction or defense function is commonly suggested for male loud calls, though actual direct evidence is quite sparse (reviewed in Snowdon 2004; Delgado 2006). The observation that loud calls evoke responses in kind (i.e. *contagion* or *counter-calling*) is often taken as evidence of their function in territorial maintenance (e.g. Hohmann 1990; Mitani & Nishida 1993; Mitani & Stuht 1998; Steenbeek et al. 1999; Zuberbühler 2002), with contagion of calls by males suggested to allow assessment of rivals (Bradbury & Vehrencamp 1998). Though a reasonable inference, this hypothesis is rarely tested and there may often be alternative explanations for observed patterns. In baboons, for example, calls in response to predators typically elicit similar calling bouts in other groups (Byrne 1981), suggesting that contagion might be a function of predator avoidance rather than (or in addition to) spacing. A mate attraction function is likewise suggested for primate loud calls (Waser & Waser 1977; Steenbeek et al. 1999; Delgado 2006), yet, clear evidence of a direct relationship between loud calls and female

reproductive behavior is practically non-existent. In some species, females preferentially approach the loud calls of some males (e.g. orangutans, *P. pygmaeus*, Galdikas 1983; Setia & van Schaik 2007); however, there might be other benefits to maintaining proximity to males (e.g. predator protection, infanticide avoidance) and thus phonotaxis alone cannot confirm a mating function for loud calls (Delgado 2006; Setia & van Schaik 2007). A function in mate attraction is often inferred from similarities to bird and anuran calls in terms of usage or propagation distance (Andersson 1994) as well as circumstantial evidence consistent with an advertisement function (e.g. unmated male gibbons sing for longer periods and have faster call rates than paired males, Cowlishaw 1992; male orangutans call more when alone than when with a female, Mitani 1985); a clear relationship between calling behavior and receiver response, however, is required to confirm function.

4.3.3 Predator avoidance In practically all sound-producing animals, some vocal signals are associated with avoiding predators and are often collectively termed "alarm" calls. Benefits from vocalizing in the presence of a predator are generally thought to be either direct, in that they reduce the signaler's likelihood of being killed (Charnov & Krebs 1975), or indirect, in that they reduce the likelihood of kin or mates being killed (Maynard Smith 1965). The mechanisms by which calls achieve these functions may differ amongst and even within species. In most birds and mammals, predator associated signals are considered to function by diverting predators from kin or group mates by attracting attention ('pursuit invitation' hypothesis; Smythe 1970), evoking predator avoidance behavior in conspecific receivers, or dissuading predators from continuing a

hunt by alerting them they have been noticed ('perception advertisement' hypothesis) (Sherman 1977; Woodland et al. 1980). Diana monkeys (*Cercopithecus diana*), for example, call in response to predators that depend on surprise (e.g. eagles) but not 'pursuit' predators (e.g. chimpanzees), consistent with the perception advertisement hypothesis (Zuberbuhler et al. 1997,1999). Male Thomas's langurs (*Presbytis thomasi*) call in response to tigers when in a group but not when alone (Wich & Sterck 2003), suggesting calls function primarily to warn conspecifics.

4.3.4 Multiple Receivers, Multiple Responses In communication research, signals are conventionally regarded as exchanges between a signaler and a single receiver, a dyadic framework that leads to characterization of signal function from a single class of respondent. Though useful for empirical study, this model does not address the reality that many signals, especially in highly social species, are broadcast in networks of multiple receivers (McGregor & Peake 2000) that likely differ in age, sex, reproductive state, and social status. The fitness relevance of a particular signal, and thus what constitute adaptive responses, therefore may differ among receivers. In response to male red deer roars, for example, rival males may retreat (Clutton-Brock & Albon 1979) or roar back if similar in size (Reby et al. 2005), whereas females may approach (McComb 1991). Signals that evoke different responses in different receivers are found across taxa (reviewed in Berglund et al. 1996), suggesting that traditional linear models used to define "*the* function" of a signal are perhaps insufficient. Though selection should favor specificity of receiver response in some cases (e.g. predator alarms), the efficiency of signals that function in multiple capacities should also be favored.

Recent theoretical and empirical work has addressed signals with multiple receivers, and specifically that individuals benefit by *eavesdropping* on signals *intended* for another (McGregor & Dabelsteen 1996; Cheney & Seyfarth 2005). Female great tits, for example, attend to male singing bouts and vary extra-pair copulation rates based on their mate's singing relative to others' (Otter et al. 1999). Designating "intended" receivers and "eavesdroppers" may be a practical approach to examining signals, but it presumes a deterministic model of signal function that may not be suitable for many systems. From a proximate view, "intended" implies cognitive mechanisms for signal production that have not been demonstrated in most taxa (Owren & Rendall 2001); from an evolutionary perspective, even if "intended" is used as shorthand for receivers whose response is presumed *most* beneficial to signalers, attributing function to the response of one receiver class mischaracterizes the multidimensional nature of selection.

Signals are under selective pressure based on all consequences of broadcasting that signal; research should therefore acknowledge that some signals, especially conspicuous ones in densely populated areas (e.g. primate loud calls), may evoke different responses from a variety of receivers. Functional explanations should address responses by all receivers in a signal's broadcast space, and thereby include the additive and relative influence of multiple sources of benefit to a signaler, even if these are asymmetrical.

4.4 Entire Repertoires

The vast majority of animal communication research centers on examinations of individual signals or signal classes (e.g. alarm calls), for which some particular facet of signal form, usage, eliciting stimuli, or function is described. This targeted approach can

be extremely fruitful, and provides opportunity for concise, supportable conclusions. The structural and functional diversity within entire repertoires, however, remains an important yet poorly understood topic in evolutionary biology (Johnstone 1996; Nelson & Poesel 2007). The evolutionary basis for repertoire diversification has been addressed in birds, primarily in regard to repertoire size (Catchpole & Slater 1995), yet in mammals, little has been done in this regard. Across primates, McComb and Semple (2005) found vocal repertoire size is associated with group size and degree of social bonding, and others have suggested that ecological factors influence repertoire complexity (e.g. Stephan & Zuberbühler 2008).

One of the goals of this review was to highlight the fact that vocal signals are not modular traits, but rather interconnected parts of repertoires that reflect the evolutionary history of species' communication. I strongly second Gros-Louis et al. (2008) in their assertion that a true understanding of vocal signals requires examining them in the context of species' entire repertoires. Characterizing the structural and functional diversity of repertoires as a whole, based on comprehensive examination of variation within and among signals, provides for greater understanding of signal usage and opportunities for interspecific comparison, thus providing substantial insight into how communication systems evolve and how signals relate to species' social behavior, ecological conditions, and phylogeny.

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CHAPTER 2

THE VOCAL REPERTOIRE OF ADULT MALE BLUE MONKEYS (*CERCOPITHECUS MITIS STUHLMANNI*): A QUANTITATIVE ANALYSIS OF ACOUSTIC STRUCTURE.

ABSTRACT

Species' communicative signals are key elements in understanding social behavior. Furthermore, quantified description of signal structure and usage provides a foundation for comparative studies that can illuminate socioecological factors relating to the evolution of communication systems and speciation. This study presents a comprehensive descriptive catalogue of the vocal signals of adult male blue monkeys (*Cercopithecus mitis stuhlmanni*). During 12 months in the Kakamega Forest, Kenya, I observed and digitally recorded vocal behavior of adult males across a variety of socioecological contexts. From spectrograms, I measured calls' acoustic structure using 50 temporal and frequency parameters. Using aural assessment, visual inspection of spectrograms, and undirected ordination and hierarchical cluster analysis, I identified six distinct call types by adult males: *ant*, *boom*, *ka*, *katrain*, *nasal scream*, and *pyow*. A few other, extremely variable and graded vocalizations collectively constituted < 0.2% of all vocal behavior and were excluded from subsequent analysis. Cross-validated discriminant function analysis supported the six call type classifications. The repertoire is best described as discrete, though some gradation occurs between *pyows* and *ants*. The degree of within type variation differed among calls, from extremely low (*boom*) to extremely high (na*sal scream*), potentially indicating varying degrees of functional plasticity and selection pressure. Preliminary examination of socioecological contexts of production suggests some calls relate to specific affiliative, agonistic, and predator avoidance functions.

INTRODUCTION

More than a century of research has greatly improved understanding of how animals use and perceive signals and provided considerable insight into the social and ecological factors shaping their production (Hauser 1996; Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003). Understanding of the functional implications of variation within signal complexes, and how entire communication systems operate and evolve, however, remains incomplete. Aside from the tremendous challenges of inferring the evolution of behavior, the conventional research focus on individual signals (i.e. single hypotheses tested on single signal types) bears at least partial responsibility. Understanding the ways in which species' signals are used and evolve benefits tremendously from research that acknowledges and addresses that signals are related units within an integrated suite of behavioral elements (Price & Lanyon 2002; Gros-Louis et al. 2008).

Many have asserted that systematic ethnography should serve as both "foundation and starting point of behavioral research" (DeWaal 1988). In regard to species' vocal behavior, signal repertoires are such a starting point, and serve as a critical foundation for exploring proximate and ultimate explanations for individual signals (Hauser 1996; Owren & Rendall 2001). Compiled repertoires also establish common terminology and referents for researchers to use and thus avoid unnecessary confusion and mischaracterization. Quantified signal catalogues further provide data for comparison within and among species, enabling more robust examination of socioecological factors relating to selection (Marler 1977; Owings & Morton 1998; Bradbury & Vehrencamp 1998; Owren & Rendall 2001; Maynard Smith & Harper 2003), speciation and phylogenetic reconstruction (e.g. West-Eberhard 1983; Gautier 1988; McCracken &

Sheldon 1997; Cap et al. 2008), and the evolution of complex communication systems (e.g. Price & Lanyon 2002). Over the past two decades, compiling species' signal catalogues has received greater attention, with a number of repertoires now available for species of birds (e.g. Seneviratne 2009), anurans (e.g. Vaira et al. 2011), and mammals (e.g. deer, Minami & Kawamichi 1992; dolphins, Boisseau 2005; orcas, Filatova et al. 2007; primates, Range & Fischer 2004; bats, Knörnschild et al. 2010).

Classification of signals

Cataloguing a species' vocal repertoire is fundamentally a classification, and has traditionally relied on human observers' aural and, more recently through spectrograph examination, visual assessment of differences in acoustic structure to categorize vocal signals. Implicit in this approach is that, beyond utility in characterizing patterns in data, distinctive variants in a species' vocalizations likely reflect past or ongoing selection and thus some biological reality. This reasonable assumption is consistent with general principals of signal evolution: stereotyped signals result from selection favoring distinct behavioral elements that evoke receiver responses that benefit signalers (Wilson 1975; Krebs & Davies 1993), and discriminative responses require receivers to both perceive and have a *categorical* perception of variation (Harnad 1987; Maurus et al. 1988).

Qualitative assessment as a method of classifying signals, however, is susceptible to a host of problems, stemming primarily from the fact that categories are based on similarities and differences that *human observers* perceive and assume meaningful. Even with experienced researchers and advanced acoustic technology, differences that are salient to a study species may be overlooked or ignored by researchers or, conversely,

variation that is not biologically relevant may be used to classify signal types. A classic illustration of this issue comes from primate research. During field observations of Japanese macaque (*Macaca fuscata*) vocal behavior, Green (1975) identified the "*coo*," a call easily distinguished from other calls by ear. Observations of animals' inconsistent use of and response to this "single" call type, however, led to further examination that eventually confirmed two distinct *coo* variants, distinguished by a feature nearly imperceptible to humans – the temporal position of the highest frequency – that was perceived categorically by macaques (Green 1975; Zoloth et al. 1979; May et al. 1989).

The challenges of classification should not imply that signal types are heuristics only, but they do highlight an inherent paradox: in any scientific pursuit of merit, objectivity should be paramount, yet analyses are impossible (or at least uninterpretable) without classification, a process that is inherently subjective. Though this paradox may never be fully resolved, advances in technology and analytic approaches have greatly increased the quantitative precision of signal ethograms and thus enabled greater objectivity via *post hoc* assessment. Identifying and measuring acoustic features has benefited from the emergence of more quantitative methods, including enhanced spectrographic rendering of sound and automated extraction of acoustic parameters (e.g. Schrader & Hamerschmidt 1997). Undirected, multivariate statistical methods provide a more objective approach to identifying distinct groups, and have been used in characterizing signal types in a variety of taxa; such methods include principal components analysis, spectrographic cross correlation analysis, and numerous variations of cluster analysis (e.g. Clark et al. 1987; Chabot 1988; Hammerschmidt & Fischer 1998; Cortopassi & Bradbury 2000; Wood et al. 2005). And lastly, application of *post hoc* statistical validation of categories (e.g.

discriminant function analysis, classification and regression tree analysis, multivariate analysis of variance) provides opportunity to objectively assess the appropriateness of signal classifications (e.g. Baker & Logue 2003; Range & Fischer 2004; Boisseau 2004; Melendez et al. 2006).

Quantifying variation within signal types

Among the many research benefits of categorizing signals, perhaps the most useful to evolutionary biology is that it provides a foundation for comparative analyses among individuals, groups, populations, and species. As analyses move up to species level, however, the tendency to represent signal types by single measures of central tendency can obscure the potential importance of variation within signal types. For example, comparing number of call types in species' repertoires has been used to provide valuable insight into evolutionary processes across taxa (e.g. reviewed, for birds, in Read & Weary 1992; in primate species, repertoire size, measured as the number of reported call types, was associated with level of social bonding; McComb & Semple 2005), yet the implied equivalence among discrete signals may discount the role of variation. It is reasonable to assume that variation provides functional plasticity; cases are likely to exist, therefore, in which a signal comprising a high degree of variation is functionally equivalent to a combination of several more homogenous signals, thus limiting the inferential scope of comparison based solely on absolute number. Put simply, comparison among signals is more informative when it also incorporates variation within them.

This Study

Blue monkeys (*Cercopithecus mitis*) are members of the group of Old World monkeys known as guenons. This is a large and ecologically diverse radiation that includes arboreal and terrestrial species, forest, woodland, and savanna dwellers, and a variety of social systems (Butynski 2002). In addition to improving understanding of one species, therefore, analysis of blue monkey vocal behavior provides data with which to explore vocal signals in a large radiation and examine the influence of various social and ecological factors while controlling for phylogenetic affinities.

Only a handful of researchers have explicitly examined blue monkey vocal behavior, including Estes (1991), Brown and colleagues (1984, 1989; et al. 1995), and Butynski et al. (1992), with the most detailed ethogram described by Marler (1973). These studies each contribute significantly to our understanding of the species' vocal behavior, yet a comprehensive repertoire of blue monkey calls has not been established, limiting examination of their communication system and opportunities for comparative studies across populations and taxa. Furthermore, in the decades since these studies, technological advances have provided substantial improvements in audio recording and acoustic analysis capabilities.

This chapter provides a quantified description of the vocal signals used by adult male blue monkeys (*C. m. stuhlmanni*); this species' vocal behavior is highly sexually dimorphic, and it is thus appropriate to examine males separately as well as in context of the entire species. The intention here is an objective, systematically derived vocal signal catalogue that increases our understanding of the species and the radiation to which it belongs, while also contributing quantitative data for use in future studies.

I used digital audio recordings and behavioral observations from more than 12 months of continuous fieldwork in undirected multivariate analyses and *post hoc* validation tests to 1) establish a detailed descriptive repertoire of male vocal signals and 2) characterize the relative acoustic similarity between and among identified call types. In summarizing the acoustic structure of call types, I provide general characterization of the social and ecological contexts in which different call types are used; quantitative analysis of variation in contextual use, examination of signal content, and explicit functional hypotheses for call types will be addressed in subsequent chapters.

METHODS

Study Site and Species

Fieldwork took place over 13 months (Sept 2010 – Sept 2011) in the Kakamega Forest, a semi-deciduous rain forest in western Kenya (0° 16′ N, 34° 52’ E; elevation 1,580 m; for detailed description of the site, see Mitchell et al. 2009; Fashing et al. 2012; Cords 2012). The forest supports a relatively dense population of blue monkeys (*C. m. stuhlmanni*), approximately 192 individuals per km^2 (Fashing et al. 2012), and is home to five other primate species: *Cercopithecus ascanius*, *C. neglectus*, *Colobus guereza*, *Papio anubis*, and *Perodicticus potto* (note: all but *C. neglectus* are found at the study site, though baboons are rare). There are several large raptors and snakes, including crowned hawk eagles (*Stephanoaetus coronatus*) and Gaboon vipers (*Bitis gabonica*), both of which prey on blue monkeys (Struhsaker & Leakey 1990; Foerster 2008). Though once present, leopards (*Panthera pardus*) have not been reported in the area in > 10 years.

Blue monkeys live in social groups comprising several adult females and their offspring and typically one adult male (hereafter: *resident* male). Females are philopatric and, at Kakamega, actively defend territorial boundaries during frequent aggressive intergroup encounters with neighboring social groups (Cords 2002a; 2007). Behavioral observations and birth records indicate an annual concentrated mating season of three-to-five months centered on August (Cords & Chowdhury 2010).

Males leave natal groups at around seven years old (Ekernas & Cords 2007) and live as "bachelors" (hereafter: *non-resident* males); non-resident males are found alone, in loose associations with other non-residents, or inhabiting the periphery of heterosexual social groups. Some of these males eventually become sole resident males of groups, either by expelling previous residents, sometimes quite forcefully, or filling the vacuum created by their death or disappearance. When a new male takes over a group, he may (but does not always) kill infants up to nine months old; infanticide accounts for at least 17% of infant mortality (Cords & Fuller 2010). The length of tenure of resident males is highly variable, ranging from a few months to six years (Lawes et al. in press).

The modal social structure of blue monkeys is characterized by unimale / multifemale groups. Although this social system is associated theoretically with reproductive monopoly by the resident male (Emlen & Oring 1977; Ellis 1995), the reproductive patterns of this species are considerably more complicated. Both resident and non-resident males frequently interact with several different social groups (Tsingalia & Rowell 1983) and genetic data indicate that multiple males may sire infants in a group, even during times when only one male maintains residency (Hatcher 2006; S. Roberts, unpublished data). Furthermore, in close to 25% of group years, multiple males occupy a

single social group consistently and for extended periods during the mating season and females may mate with all males in these *multimale influxes* (Cords 2000; 2002b). As the mating season ends, influxes dissipate and sole resident status is resumed, typically, though not always, by the prior resident male (Cords 2002b).

The patterns of social interaction for males participating in a multimale influx (hereafter: *influx* males) differ from those of both residents and non-residents. Due to proximity, influx males have more opportunity to interact with females than non-residents do. Relative to both residents and non-residents, influx males are more likely to interact with other males, thus likely increasing male agonism rates. Aggression among influx males is frequent, yet there appears to be greater tolerance among them than typically shown by residents for intruders; resident males predictably respond to other adult males near their groups with increased vigilance and vocalization, frequently initiating chases and physical aggression (Henzi & Lawes 1988; *pers. obs*.).

Call types reported for blue monkeys have been identified mainly from subjectively assessed distinctiveness (Marler 1973; M. Cords, pers. comm.; pers. obs.). The vocal repertoire of this species is highly distinctive among age-sex classes. Preliminary analyses suggest that adult females and juveniles of both sexes use a variety of signals that fall generally into seven categories (unpublished data): *chirps* (loud, high frequency, tonal signals with ≥ 4 distinct variants), *trill* (tonal, sinusoidal signal with variable duration and amplitude), *scream* (loud, harsh, highly variable signal with structural similarity to *trills*), *growls* (low frequency, atonal, staccato signals of varying amplitude with ≥ 4 distinct variants), *gecker* (rapid sequence of repeated short, atonal units), *grunts* (quiet, low frequency, atonal signals with possibly several variants), and *long grunt* (low

frequency, tonal signal with variable duration and amplitude). Infant vocalizations include a variety of graded signals, primarily *trills*, *girns*, and *geckers*, that are quieter than most used by older individuals. Vocal behavior of adult males is highly distinct from that of other age-sex classes, with signals being considerably louder, lower frequency, and used less often. Call types reported for adult males in this population include the *ant*, *boom*, *ka*, *katrain*, *nasal scream*, and *pyow* (Marler 1973; M. Cords, pers. comm.).

Little is known about the auditory capabilities of blue monkeys, with the best data from laboratory experiments with two juvenile subjects, one male and one female. Brown and Waser (1984) found blue monkeys were sensitive to (i.e. capable of discriminating) changes in acoustic energy (i.e. loudness) of more than 5 dB SPL. Subjects were better than humans at detecting sounds below 500 Hz and above 8000 Hz, and more sensitive to low frequency sound changes than rhesus macaques (*Macaca mulatta*).

Subjects

Subjects were 20 identified adult males, each identifiable by facial and body features. Using the mean age of natal group dispersal of 7.25 years (Ekernas & Cords 2007) as a proxy for sexual maturity, I considered males that were older than seven years adults. For subjects whose age was unknown, I relied on conspicuous physical attributes such as body size, descended testes, and elongated canines to differentiate between adults and sub-adults. Males were unequally sampled, with the vast majority of data from the resident males of five social groups that have been part of long term research on blue monkey social behavior since 1979 (Cords 2012).

Data Collection

Vocal Signal Usage

During the study period, 4-14 trained observers were in the field every day (22 days per month, ≥10 observers; 8-9 days per month, ≥4 observers). Observers were distributed among males and social groups and typically located subjects between 0710 and 0750 h and typically followed them until 1730 h. On 22 days per month, three (and occasionally four) males were each followed continuously (unless lost) for the entire day; other observers rotated 20-minute focal follows of adult females in social groups.

Data on adult male vocal behavior were collected on an all occurrence basis (Altman 1974). To distinguish levels of analysis, I use the terms *Call* to denote a single, discrete vocal utterance (e.g. one *pyow*), *Bout* to denote a repeated series of one call type with no other call types interspersed and ≤ 1 minute between calls, and *Episode* to refer to any occurrence of vocal behavior by a male and including all calls made by him with ≤ 1 minute of silence between calls; these categories are nested, such that an episode might comprise just one call (e.g. one *boom*), a bout (e.g. five *pyows*), or combinations (e.g. one *boom* followed by five *pyows* followed by two *ants*). Most episodes consisted of only one call type, given singly or in bouts, but combinations were not uncommon.

Whenever a male vocalized, observers recorded the time and call type(s), the caller's identity and location, and the social and ecological context in which the call occurred. Context was recorded narratively, noting the caller's activity just before and just after calling, the general activity of other monkeys in the vicinity (e.g. feeding, moving, alarm behavior), and conspicuous social (e.g. affiliative interaction, presence of other male) and

ecological factors (e.g. predators, tree fall). When appropriate, observations by several observers were combined to provide more complete assessment of context.

As the present study was focused on the acoustic structure of vocalizations, call usage was characterized qualitatively; quantitative analysis of the relationship between call usage and context, including data from playback experiments, is provided in Chapter 3. Conservatively using only call records in which the context could be clearly determined, I characterized the degree to which different call types are associated with particular social and ecological contexts by examining the proportion of each call type's occurrence in different contexts. I also examined the proportion of episodes that included each call type to assess the relative usage of each call type.

Digital audio recordings

I recorded vocalizations with a Marantz PMD-660 solid state digital recorder set at a sampling rate of 44.1-kHz (16 bits), with a Sennheiser ME67 directional microphone. Recordings were made during systematic 3-hour focal samples, during playback experiments, and opportunistically throughout the study period. Distance to callers varied from as close as five meters to more than 400m. Adjusting microphone input level (i.e. gain) reduces differences in recording quality when distances and obstructions are small, but signals can become substantially attenuated if transmitted over long distances; I therefore excluded from analysis recordings made >100m from the caller.

Acoustic analysis

The initial audio sample, extracted from more than 450 recording hours, comprised 1171 recordings of calls by ≥ 27 males. Each recording sample was initially classified

according to aural consistency with one of six call categories: *Ant*, *Boom*, *Ka*, *Katrain*, *Nasal Scream*, and *Pyow* (three other vocalizations that constituted less than 0.2% of adult male vocal behavior during the study period were excluded; see Results). Some call types were frequently given in bouts, and qualitative assessment suggested that calls become increasingly quieter, less tonal, and shorter as bouts continue; sequences of more than five *pyows* or *katrains* and fifteen *ants* were rare, and I therefore excluded call samples beyond the fifth and fifteenth. After also excluding lower quality recordings (e.g. overly quiet, disrupted by sounds from birds, insects, or other monkeys) and those from unidentified callers, 772 recordings of calls by 20 males remained. The number of recordings of each call type differed and different individuals contributed different numbers of call samples (Table 1).

I used Raven Pro 1.3 (Cornell Laboratory of Ornithology, Ithaca, New York) to perform discrete Fourier transform (Hann window function, 1024-pt DFT, 20 ms window size, 46.9 Hz frequency resolution) on digital recordings. With resulting spectrograms, power-time oscillograms, and power-frequency spectra, I used a visualizing window of 0.5 seconds and frequency range of 0-3000 Hz (for the extremely low frequency *boom* call, I used a visual frequency range of 0-1000 Hz). The following is a general description of the acoustic parameters and methods used to extract them, with more details provided in Table 2 and illustrated in Figure 1.

Of all the call types, only *katrains* comprise multiple distinct units or 'syllables' (see Results). The acoustic variable "number of units," therefore, unambiguously distinguishes *katrains* from all other calls yet has no discriminatory value among other types. The multi-unit structure posed other problems in comparative analysis, as each

katrain contains multiples of acoustic features (e.g. frequency bands) that are singular in other calls. To address these issues and examine the structure of individual units of *katrains*, I used three individual units (second, middle, and second to last) from each *katrain* as samples for analyses. In Results, I provide summary descriptions of individual units and the entire call for *katrains*.

For each call sample I measured 50 acoustic parameters, addressing the total call and three distinct structural elements within the call: the fundamental frequency band (F0), the first dominant frequency band above F0 (DF1), and formant dispersion (i.e. distance between frequency bands). In communication literature, the terms *formant* and *frequency band* are often used interchangeably to describe areas in a call's spectrum where energy is concentrated in adjacent harmonics; these result from resonances in the vocal tract and are identified from dark bands in spectrograms and peaks in frequency-power spectra.

Temporal and frequency limits of the total call were determined using the power-time oscillograms (waveform view) and frequency-power spectra at single times (spectrogram slice view) to identify energy above ambient noise. To avoid conflating echo with source signal, I used the terminus of the F0 (in spectrogram) and emergence of a repeating oscillation pattern (in waveform) to identify the end of calls (see Fig. 1). The first three dominant frequency bands (F0, DF1, and DF2) were identified by consistent energy peaks in consecutive frequency bins. The start, middle, and end frequencies were identified as the frequencies at which maximum power (peak amplitude) occurred in the first, middle, or last quartile, respectively, of the call or band. Slopes (i.e. rates of frequency change) were calculated by plotting the start, middle, and end frequencies against duration. Rises were the interval from the start time to the time at which

maximum power (peak amplitude) first occurred. The central frequency was the frequency that split the total call into frequency intervals of equal cumulative energy.

To calculate formant dispersion (i.e. the distance between dominant frequency bands), I first selected several time points (median: 4; range: 3-7) across the call in which the F0, DF1, and DF2 could be unambiguously identified. At each time point, I subtracted the maximum frequency (frequency at which maximum power / peak amplitude occurred) of the F0 from that of DF1 to derive formant dispersion ($FDisp\_1_i$) and repeated the process with the second and third bands ($FDisp\_2_i$). Mean formant dispersion for each call was the average of the formant dispersion measures.

Statistical Analyses

I used acoustic measurements to examine relationships among individual call samples and among identifiable clusters of samples, and evaluated the validity of call type categories. All statistical analyses were conducted using R version 2.1 (R Development Core Team 2008), and tests were 2-tailed using $\boldsymbol{\alpha} = 0.05$ unless otherwise specified.

To address high correlation among parameters and increase the explanatory value of results, I reduced the number of acoustic variables for analyses. I derived a Pearson's correlation matrix, using all samples and parameters, and removed variables, conservatively, so that no pair had an *r* value exceeding ±0.75 (see Results, Table 6).

Principal Components Analysis and Cluster Analysis

To characterize acoustic similarity among call samples, I used ordination and cluster analysis with all samples; *a priori* call categories guided interpretation of observed

patterns. Separation among samples was examined using principal components analysis (PCA). PCA identifies linear combinations of variables, or *principal components*, that maximally account for the variability in a data set, reducing the total parameters to a subset of uncorrelated combinations (Jolliffe 2003). Because large value differences among variables (e.g. Center frequency ranged from 107-2497 Hz, whereas Duration ranged from 0.031-0.692 secs) can exaggerate variability and thus compromise the explanatory value of PCA, I used scaled unit variance for parameters.

To characterize groupings of samples and distances between call types, I performed an agglomerative hierarchical cluster analysis (i.e. connectivity-based clustering) on the principal component scores of all samples. A Euclidean distance matrix was first used to calculate dissimilarity between samples and then Ward's linkage (Ward 1963) was used to group samples according to similarity of PC scores.

Discriminant Function Analysis

To assess the appropriateness of *a priori* call categories, I used discriminant function analysis (DFA). DFA identifies *discriminant functions*, linear combinations of predictor variables that best distinguish among preset groups, and then uses them to reclassify samples (Klecka 1980). The degree to which samples are "correctly" assigned can be used to validate predetermined groups and identify variables that best discriminate among groups.

An unbalanced data set can influence DFA adversely and I therefore randomly selected equal numbers of each call type from different males. I used a forward stepwise linear discriminant procedure, with call type as the grouping variable and acoustic parameters as predictor variables, to construct linear discriminant functions (LDs).

Stepwise DFA constructs a model in *n* sequential steps ($n = G\text{-}1 \times V\text{-}1$, where G is the number of groups and V the number of predictor variables). At each step, all variables are evaluated and the one that best discriminates among groups is added to the model. To cross-validate the resultant LDs, I used the *leave-one-out* classification procedure, using all samples except the one being classified, to assign samples to call types.

To explore differences among call types and identify specific acoustic variables that best distinguish among call types, I examined the LDs and their canonical roots. In short, I assessed the discriminatory power of each LD from the proportion of variance among call types it explained, and identified acoustic variables that contributed most to each LD from canonical root values (similar to factor loadings in PCA, *roots* refer to eigenvalues associated with each LD that specify the contribution of each variable to each LD).

RESULTS

Careful examination of recordings (n=772) and field observations (n= 9427 vocal episodes) identified nine distinctive vocalization types ever used by adult male blue monkeys: *Ant*, *Boom*, *Gecker*, *Grunt*, *Eern*, *Ka*, *Katrain*, *Nasal Scream*, and *Pyow*. The *gecker* and *eern* were each observed only four times, constituting <0.1% of all observed male vocalizations, and *grunts*, observed only six times by one male, also constituted <0.1%. The extremely small sample size made inclusion of these three vocalizations in quantitative analyses imprudent, but they are included in summary descriptions, below.

Principal components analysis

The first three principal components (PC1-PC3) captured 72% of the sample variance (Table 3), with PC4-PC5 capturing an additional 11%. PC1 was heavily influenced by several variables, but primarily frequency measures (formant dispersion, center frequency). PC2 was driven by variation in calls' rise (i.e. time to peak amplitude) and total duration. PC3 was dominated by calls' slopes (i.e. changes in frequency over time).

Plotting samples in principal component space revealed patterns consistent with *a priori* call types, yet illustrated that acoustic separation among types is not equal (Fig. 2). Three distinct clusters were easily segregated by PC1 and PC2, with *booms* and *nasal screams* each separate from others while *ants*, *pyows*, *kas*, and *katrains* agglomerate in a wide cloud. Closer examination of this cloud revealed that *pyows* cluster distinctly from *kas*, *katrains*, and *ants*, though the *pyow* cluster shares an overlapping boundary with *ants*. *Kas* and the individual units of *katrains* are intermingled with only slight separation, indicating an acoustic affinity approaching equivalency (but recall that *katrains* are distinguished by the multi-unit structure). *Ants* exhibit somewhat distinct clustering, but samples are spread wide and with notable overlap with *kas*, *katrains*, and *pyows*.

In addition to differences in between-cluster distances, PCA revealed differences in within-cluster variation (Fig. 2). The cluster containing all *booms* is the most tightly configured, reflecting an acoustic homogeneity contrasting with the variation observed in *nasal screams*, *ants*, and *pyows*.

Cluster analysis

The results of hierarchical cluster analysis, represented graphically in a dendrogram (Fig. 3), were consistent with the above patterns and provide quantitative distances between and among call types. Calls cluster into four distinct categories: *booms* only, *nasal screams* only, the majority cluster of *pyows*, and a cluster containing *ants*, *kas*, *katrains*, and the remaining *pyows*. The *booms* cluster was by far the most segregated; the distance of *booms* from all other calls was seven times that of any other nearest join and ten times that of the average join distance of calls excluding *booms*; the next largest distance is that of *nasal screams*, followed by a cluster containing the majority of *pyow* samples. *Pyows* were segregated into two different clusters, reflecting high sample variation and potentially suggesting the potential for dividing this singular call type into two. *Kas* and *katrains* clustered together, distinct from yet overlapping with *ants*.

Differences in branch lengths within clusters allows quantitative comparison of the variation within call types. The smaller cluster of *pyows* had the longest average branch length (ABL), more than three times that of *booms*, which had the shortest. The larger *pyows* cluster had the second longest ABL, followed closely by the *nasal scream* cluster.

Discriminant function analysis

The discriminant functions classified 79.5% of call samples to their named call type (cross validation = 79.3%), considerably better than the 16.7% expected by random chance (Table 4). This indicates that the acoustic variables used are sufficient to differentiate call types and suggests that *a priori* call types are appropriate. The probability that a call sample would be correctly assigned varied among call types.

Correct classification of *booms* and *nasal screams* was 100% and *pyows* 85%, whereas *ants*, *katrains*, and *kas* were all lower (69%, 77%, and 46%, respectively).

The probability that a sample was assigned incorrectly to a particular call type was associated with call type. Most (75%) misclassified *pyows* were classified as *ants*. All misclassified *katrain* units were classified as *kas* and, similarly, 86% of misclassified *kas* were classified as *katrain* units. Most (87%) misclassified *ants* were classified as either *kas* or *katrain* units.

The first two linear discriminant functions (LD) collectively explained 91.4% of the variance among call types (LD1: 54.8%; LD2: 36.6%; Table 5). LD1 correlated strongly with calls' total duration and LD2 correlated most strongly with calls' rise (i.e. time to peak amplitude) and total duration.

Descriptive Summary of Call Types

In summary statistics for each call type, an unequal contribution of samples by different males would give some individuals greater influence on the characterization of some call types. To control for this, I followed Gros-Louis et al. (2008) and derived mean values for acoustic variables for each call type for each male and then summarized call types using the pooled sample of the averaged males' calls. The following provides summary descriptions of each signal in the adult male vocal repertoire, with each call type described in regard to perceived sound characteristics and patterns of usage, with exemplar visual representations (spectrograms, power-time oscillograms, and frequency-power spectra) provided (Fig. 4-11). Table 6 summarizes the acoustic structure of each call type in terms of the acoustic parameters used in analyses.

Call Type: Ant (Fig. 4)

Sound characteristics: short, harsh, nasal sound, with an abrupt clipped nature. *Ants* are easily distinguished by ear from other call types, though "*pyowish-ants*" or "*antish-pyows*" are common in episodes in which *pyow* bouts transition to bouts of *ants*, highlighting the acoustic similarities of the two calls and suggesting grading or possibly a transitional form between *pyow* and *ant*. Though structurally similar, "definitive" *ants* are distinguished from *pyows* as being shorter, less tonal, and quieter.

Usage: Typically given in bouts with calls separated by ~8-15 seconds. Number of *ants* in a bout varied widely, from 1 – >300 (median: 21). *Ants* were given alone, but frequently occurred in combination with *pyows*, and then typically at the end of longer bouts of *pyows*. Usage was low, occurring in less than 2% of all observed episodes, but a clear relationship between *ants* and terrestrial predators was demonstrated. In *ant* observations in which context was clearly known (n=67), dogs or snakes were present in 53%, and in another 16% the caller was agitated while oriented toward an unseen terrestrial object. Other known contexts include male-male aggressive encounters (19%) and the presence of terrestrial mammals including palm civets (*Nandinia binotata*) and baboons (*Papio anubis*).

Other: In contexts in which adult males produced *ants*, females and juveniles commonly produced *chirps* and *growls*. Sympatric adult male redtail monkeys (*Cercopithecus ascanius*) also produce nearly identical *ants* in similar contexts (unpublished data).

Call Type: Boom (Fig. 5)

Sound characteristics: extremely low frequency, tonal, and similar to the sound of hitting a tub with a padded mallet. The call's acoustic features combined with the species' auditory faculties indicate *booms* may be audible to other blue monkeys as far away as 1,000 meters (Brown 1989). Human observers, however, have difficulty hearing *booms* sometimes from even as close as 40 meters and, relative to other call types, have greater difficulty judging the location of unseen callers.

Usage: Almost always given singly, though one subject (Tip) often "double *boomed*," giving a second *boom* within 15 seconds after a first; similar behavior has been observed, infrequently, in other males in previous years (Cords, pers. comm.). *Booms* were typically given by themselves, though episodes in which a *boom* was followed shortly by *pyows* were frequent enough to suggest a possible pattern. *Booms* were the most common call, constituting 50% of all episodes; their actual occurrence, however, may be slightly higher as *booms* are more likely than other calls to be missed.

Observations indicate *booms* relate to interactions between males and female group members, though the long audible distance suggests they may function in extra-group relations as well. In observations in which context was clearly known (n=1255), 23% were cases in which a male approached or was approached by females, then *boomed*, and then was groomed or fed with group members. An additional 29% of *booms* also occurred after an approach, though these contexts were less definitively affiliative, occurring during aggressive encounters with other groups or other times when groups were exhibiting high arousal. The next most common context, notably different from the

previous, was branches falling nearby or trees falling at a distance (9%); though deemed disturbance, these cases did not relate to any substantive threat to callers or group members. Other contexts included snakes, inter-group aggression, and unknown contexts that included intense vocal and arousal behavior by members of callers' groups.

Other: In approach contexts, adult females and juveniles typically produced *long grunts* – long, low frequency vocal signals used only around adult males – prior to the male's *boom*, strongly suggesting a social stimulus and possible antiphonal relationship. As in other *Cercopithecus* species that produce similar calls (e.g. *C. neglectus*, *C. campbelli*), *booms* undoubtedly depend on activation of a supralaryngeal air sac (Gautier 1971; Hewitt et al. 2002). The physiology of *boom* production may be illuminated by the distinctive postural behavior that accompanies them: when producing *booms*, males sit upright, hunch the body forward with head facing downward, quickly swell at the thorax, and *boom* with the mouth facing down and completely or nearly closed.

Call Type: Ka (Fig. 6)

Sound characteristics: short, abruptly clipped, and with a "hollow" character. *Kas* sound similar to *ants*, but are distinguished by ear as louder, more tonal, and of lower frequency.

Usage: *Kas* were rarely given alone, with > 85% occurring in episodes with *katrains* – typically with one or two *kas* preceding *katrains* by five to ten seconds. When the same male gave multiple *katrains* in an episode, *kas* commonly were given in the ten to fifteen

seconds separating them. Usage was low, occurring in only 3% of all observed episodes. Context of calling was identical to that of *katrains* (see below), and indicates a relationship with predators. In the relatively few cases in which *kas* were not followed by *katrains* or other calls, contexts included tree falls and similar disturbances.

Other: In contexts in which adult males produced *kas*, females and juveniles commonly produced *chirps* and *growls*. Acoustically, *kas* are virtually identical to individual units of *katrains* (see below).

Call Type: Katrain (Figs. 7, 8)

Sound characteristics: loud, long string of pulsed repeat units, with abrupt onset and maintaining constant amplitude and tone throughout the sequence. As the name suggests, the *katrain* sounds like (and structurally is) a rapid sequence of *kas* (above), with each unit separated by a short, guttural "*urrr*" sound. The *katrain* is the only vocal signal used by adult males that has a multi-unit structure. Due to the long duration, repetitive structure, and high amplitude, human observers can typically perceive *katrains* and reliably approximate caller location, even from more than 250 meters.

Usage: The number of *katrains* in an episode varied, but was typically one to three. *Katrains* were given alone but most commonly were accompanied by *kas* (above), and sometimes by *pyows*. Usage was low, accounting for only 4% of all observed calls, but a relationship between *katrains* and predators is unambiguous. Of 157 observations in

which context was clear, raptors were seen in 59% and in another 23%, group members' behavior was consistent with aerial predator avoidance (i.e. looking up, diving down, hiding in branches, etc.). Other known contexts include trees falling near caller (8%) and dogs nearby (3%). Note: the small proportion of *katrains*, *ants*, and *kas* relative to *booms* and *pyows* may relate to the formers' association with predators in at least two ways: predator events are likely less frequent than social interactions that evoke vocal behavior, and the presence of human observers likely reduces predator events but, for the well habituated subjects, not social interactions.

Other: In contexts in which adult males produced *katrains*, females and juveniles typically produced *chirps* and *growls*, and exhibited predator avoidance behavior, including females with infants collecting their infants upon hearing the call. *Katrains* were also associated with predator-consistent vocal behavior by other species, including *roars* by colobus monkeys (*Colobus guereza*), *chirps* by redtail monkeys (*Cercopithecus ascanius*), and extended shrieks by hornbills (*Bycanistes subcylindricus*). Consistent with both contagion and the flight patterns of raptors, *katrains* by different males frequently gave the impression of "spreading" across the forest.

Adult females in the study population have been observed to use a vocalization that, though easily distinguished from, bears resemblance to the *katrain* and is dubbed a "*female katrain*." This call is exceedingly rare; only two recordings were obtained, making comparative analysis difficult. The two calls share a similar structure of repeating units, though male *katrains* are considerably lower in frequency, louder, and longer.

Kas and katrains: Although strong relatedness between the male *ka* and *katrain* is clear from their affinity in both acoustic structure and usage, these constitute distinct call types rather than variants of a single, graded call type. Graded (*sensu* Marler 1975) signals lack distinct boundaries, displaying more or less continuous variation between classes. Field observations, however, included only *kas* produced singly and *katrains* of at least seven combined units (mean: 15), rather than increasing numbers of sequentially combined *kas*. Furthermore, the *urrr* sound linking units in *katrains* was never observed in recordings of *kas* given singly.

Call Type: Nasal Scream (Fig. 9)

Sound characteristics: harsh, nasal, rasping vocalization, exceptional in both its acoustic variability and unpleasantness. Very short (~0.1 secs) *nasal screams* were sometimes observed, but calls were typically longer (~0.5 secs), rising in both frequency and amplitude in the middle of the call. Comprising higher frequencies and lower amplitude than other male calls, *nasal screams* are difficult for human observers to hear from farther than ~50m.

Usage: *Nasal screams* were rare, observed only 11 times during this study (<1% of all vocal episodes). Usage was unambiguously associated with intense aggression between males. Though resident males encountering "intruder" males often threaten and chase, *nasal screams* were observed only during the rare interactions that included intense physical contact or, with males facing off in close proximity, when such contact appeared

imminent. Typically only one of the combatants *nasal screamed*, usually the recipient of the aggression or putative "loser"; a very few observations in past years have included a male *nasal screaming* while attacking (M. Cords, *pers. comm*.).

Accompanying vocalizations: In some particularly intense encounters, *nasal screams* were interspersed with other utterances. Among a few unclassifiable sounds, two of these were somewhat distinguishable, named here *eerns* and *geckers*. In contrast to other call types, these were very quiet, characterized by high central frequencies, and exceptionally rare; they are described here and in Figure 11 based on the three available recordings.

> ***Gecker***: rapid sequence of nearly identical repeated units that are extremely short and raspy, with no detectable sound between pulsed units (see *katrains*, above).
>
> ***Eern***: quiet, nasal, and with a slight tonal quality, *eerns* are extremely variable in duration, and are possibly shortened forms of *nasal screams* produced with a partially or fully closed mouth.

Other: Of adult male signals, the *nasal scream* and the graded vocalizations sometimes accompanying it bear the most structural similarity to signals used by adult females and juveniles of both sexes. Though considerably louder, longer, harsher, and spanning a larger frequency range, *nasal screams* by adult males are structurally similar to *screams* by adult females during aggressive encounters; these *screams*, in turn, appear to be highly graded and intensified versions of commonly used *trills* (unpublished data). Additionally, *geckers* by adult males were structurally consistent with signals used by adult females and juveniles of both sexes; female and juvenile *geckers* typically occur in agonistic

encounters and appear to function as submissive gestures (unpublished data). Finally, the highly graded *eerns* observed in adult males, though louder and more spectrally dynamic, resemble the *girns* used by infants, typically when denied suckling by mothers (unpublished data).

Call Type: Pyow (Fig. 10)

Sound characteristics: loud, tonal, and with a relatively slower onset and longer duration than other call types. The long duration and negative slope (i.e. drop in frequency from start to finish) gives *pyows* a characteristic "descending" sound. Acoustic similarities to *ants* are discussed above. *Pyows* vary considerably among individuals, with experienced observers able to distinguish some individuals by hearing their *pyows*. With its high amplitude and modulating frequency, as well as the tendency to occur in repeated bouts, human observers can typically perceive a *pyow* and reliably approximate caller location, even from >300 meters.

Usage: Typically given in bouts of 3-4 *pyows* (range 1-16), each separated by ~10-15 seconds; the last *pyow* in a bout typically had a longer intercall interval than those preceding it. *Pyows* were most often given alone, but episodes in which *pyows* were in combination with *ants*, *booms*, or *katrains* were not uncommon. *Pyows* were the second most frequently observed call, constituting 41% of episodes.

Contexts varied considerably, and observations in which context was clearly known (n= 1174) fell into two contrasting categories: disturbance and non-disturbance.

Disturbance contexts related to predators (dogs, unfamiliar humans, or group behavior consistent with terrestrial predators, 19%; raptors seen or group behavior consistent with aerial predators, 7%) or male-male agonism (after chasing another male, 12%; when another male was nearby and the caller continuously oriented, scanned, and moved in his direction before and after calling, 15%; or during aggressive intergroup encounters in which another male was present, 31%).

Although it is difficult to gauge the degree to which an animal is "not disturbed," nearly 12% of observations of *pyows* occurred when there had been no observed aggressive interaction, predator or predator related behavior, or other male or group nearby; in these contexts, behavior by the caller and nearby group members before and after calling did not reflect high arousal or vigilance, and callers typically resumed feeding or resting after calling. Such observations are consistent with "spontaneous" calling linked to territorial advertisement and mate attraction functions in some mammals and birds (e.g. deer, Clutton-Brock et al. 1979; primates, Grassetto & Byrne 2006; birds, McGregor & Dabelsteen 1996).

Other: Grunt (Fig. 11)

One other vocalization by one adult male (Sawa) was observed during the study period. *Grunts*, like the *eerns* and *geckers* (described with *nasal screams*, above), were so exceedingly rare – only six times in 12 months, or <0.1% of all observed male vocalizations – that inclusion in the adult male repertoire is not warranted.

Grunts were short, quiet, pulsatile, generally atonal vocalizations, similar to clearing one's throat. These were observed in only one male, and then only in contexts in which he appeared calm and group members were feeding and moving around him; on three occasions, he *grunted* before he *boomed* several seconds later.

Other: Notably, *grunts* used by the one adult male were structurally consistent with *grunts* by adult females and juveniles of both sexes. These signals are used frequently and in a variety of social interactions and appear to relate generally to affiliative or cohesive behavior among group mates (unpublished data).

DISCUSSION

Call types

From more than 6,000 observation hours of 30 subjects, I summarized the vocal repertoire of adult male blue monkeys into six primary call types: *Ant*, *Boom*, *Ka*, *Katrain*, *Nasal Scream*, and *Pyow*. Three additional vocalizations – *Gecker*, *Grunt*, and *Eern* – were used so rarely that it is difficult to determine whether these calls constitute anomalous behavior or stable but extremely rare signals in the male repertoire (though appearances strongly suggest the former). Each call type is distinguishable by ear and by visual inspection of spectrograms, and distinctiveness consistent with *a priori* call categories is supported by quantified analyses. As Range and Fischer (2004) noted, however, it is the researcher's choices of methods, inclusion, and partition that

determines the number of call types described for any repertoire, a number, therefore, that may be more an organizing convenience for research than a claim of biological reality.

The 20% failure of discriminant function analysis in distinguishing among call types misrepresents the overall distinctiveness of the repertoire, as it is driven mostly by the apparent difficulty to correctly classify *kas* (46%) and *katrains* (77%). Examining the specific assignments (i.e. the call types to which samples were incorrectly assigned), all *katrains* and 92% of *kas* were classified as either *katrains* or *kas*, confirming the acoustic similarity of *kas* and individual units within *katrains*; recall, however, that *katrains* are multi-unit calls and are unmistakably different from other call types. In fact, if *kas* and *katrains* are considered one call type in analysis, the overall accuracy of DFA is 90%.

Pyows are well distinguished in DFA (85% correct assignment), and confused mostly with *ants*; this again highlights the acoustic affinities between *pyows* and *ants*, and supports the possibility of a grading, transitional form between the two call types. In the dendrogram, *pyows* fall into two distinct clusters – a majority cluster that is cleanly diverged from all others, and another group constituting a sister cluster to *ants* and *kas* (Fig. 4). The existence of two *pyow* clusters may be an artifact of the large sample size and inherent variation relating to individual male differences; considering the variety of contexts in which *pyows* occur, however, acoustic differences may reflect functional variation. These possible explanations will be examined in Chapter 3.

Relative to some vertebrate taxa, the vocal repertoire of adult male blue monkeys is small (e.g. the song repertoire of brown thrasher, *Toxostoma rufum*, exceeds 1,000, Boughey & Thompson 1981; orcas, *Orcinus orca*, use at least 26 calls, Dalheim & Awbrey 1982); the repertoire, however, is similar in size to those described for many

other primates (reviewed in McComb & Semple 2005) and call types bear strong acoustic similarities to some described in males of other *Cercopithecus* species (see below). The small repertoire of male blue monkeys, along with a generally low rate of calling relative to females (unpublished data), likely reflects their limited social interactions and may constitute functional constraints on male vocal behavior. Variation in acoustic features within call type, however, may expand the functional capacity of this repertoire, and combining call types in sequences may also create unique functional categories. The use of *booms* closely followed by *pyows*, for example, may be similar to a pattern Zuberbühler (2002) observed in Campbell's monkeys (*C. campbelli*) in which experimental playbacks demonstrated that *booms* given just before another call type resulted in different behavioral responses by receivers than either call given on its own.

Repertoire structure

Cluster and discriminant function analyses support discrete call types, but the degree to which call types are distinct from others varies across the repertoire. In all analyses, *booms* and *nasal screams* were unambiguously distinguished from all others, with other call types much more closely associated. These results, along with a quick look at the spectrograms, suggests the male repertoire is built on three primary acoustic structures, with the incontestably unique multi-unit structure of *katrains* constituting a fourth.

The primary structure in the repertoire, exemplified by the *pyow* (Fig.11), is two to three clearly defined frequency bands (F0, DF1, DF2) tracing an even, downward slope, with increasing turbulence (i.e. noise) in higher frequencies. *Ants, kas*, *pyows*, and the individual units of *katrains* all share this basic structure, suggesting a common

physiology of production (Fitch & Hauser 1995) and that only minimal vocal modification is required to produce the distinctive variation in duration, center frequency, and slope. The structure of *nasal screams* differs substantially, exhibiting more harmonic evenness and energy concentrated in higher frequencies, but it is its "rise and fall" sound (seen in the bell shape of spectrograms) and extreme variation in duration that best distinguishes it to human observers. The *boom* is fundamentally different from all other calls, with center frequencies nearly ten times lower than those of other calls and a conspicuous absence of harmonics; both these features reflect reliance on the supralaryngeal air sac (Gautier 1971; Fitch & Hauser 1995), with the latter suggesting *booms* may not resonate through the vocal tract at all.

Variation

The presence of different call types undoubtedly reflects selection pressure on vocal behavior favoring distinctiveness. The mechanisms by which such selection might arise are many, but are likely to relate generally to differences in callers' arousal level (Morton 1977), receivers' innate neurophysiological responses to acoustic features (Owren & Rendall 2001), the degree to which vocal variants are associated with specific contexts (Seyfarth & Cheney 2003), and constraints associated with physiology of sound production (Fitch & Hauser 1995) and ecological factors associated with sound transmission (Mitani & Stuht 1998).

In addition to variation sufficient to distinguish among call types, variation within types is likely relevant to both past and present selective pressures. All call types exhibit variation in several acoustic features, providing ample room for acoustic variation to

relate to specific caller attributes such as identity, age, body size, and particular arousal level or behavioral or social context. Such plasticity is most apparent in *pyows*, the most contextually and acoustically variable of all call types. In contrast, *booms* exhibit the least structural variation, relating most likely to the physiology of production and possibly imposing constraints on the call's functional range.

The consistency with which *kas*, *katrains*, and *ants* are contextually associated with predators, coupled with the general distinctiveness of call types, provides opportunity for these calls to be functionally referential (Harnad 1987; Seyfarth & Cheney 2003); given the contextual specificity of use, the variation within these call types may relate more to individual differences in callers or simply a lack of selection on more uniform acoustic structure. The acoustic similarity and near complete overlap in contextual usage between *kas* and *katrains* likely indicates common production mechanisms, origin, and function(s). It may be that a functionally meaningful arousal or physiological threshold relates to whether a male *kas* only or transitions to *katrains*, or that selection favored the highly distinctive structure of the *katrain* but did not select against its shorter antecedent; more research is necessary to explore selection for the multi-unit structure of *katrains* and the retention of what appear to be redundant call types.

Functional implications of structure

In addition to providing metrics for distinguishing among signal types, acoustic features can offer insight into function, with inference drawn from identified relationships between structure and the way signals are perceived and influence receiver response.

A vocalization's active space (i.e. distance from signaler at which conspecifics can hear the signal) provides a sense of how many individuals and of what age-sex classes are potential receivers. Very quiet calls, for example, are likely to function in dyadic interactions between animals in close proximity, whereas signals with long audible distances can potentially achieve multiple functions in both within- and between-group communication (e.g. mate defense, spacing, mate attraction; reviewed in Wich & Nunn 2002). In a series of laboratory experiments, Brown and colleagues used the auditory sensitivity of blue monkeys, the acoustic structure of some call types, and the sound attenuating characteristics of an "average" rain forest to calculate calls' audible distances (Brown & Waser 1984; Brown 1989; Brown et al. 1995). Their results, in context with field observations in Kakamega, indicate that *pyows*, *booms*, *kas*, and *katrains* can be heard by all members of the caller's social group as well as members of several adjoining groups and non-resident males: calculated audible distance for *pyows*, *booms*, *kas*, and *katrains* was ~1,200m, ~900m, ~700m, and ~600m, respectively (Brown 1989), whereas the home ranges of the five primary groups in my study had an average longest axis of 839m (range: 547-1223; unreported data). Though not evaluated in Brown's study, *ants* and *nasal screams* have relatively lower amplitude and less energy concentrated in low frequencies, indicating shorter audible distances and functions likely limited to interactions with more proximate animals.

The relative localizability of a call (i.e. degree to which perceivers can accurately gauge call origin) also has implications for how receivers could respond and how selection might have shaped structure. In cases in which signalers benefit if receivers approach directly (e.g. mate attraction, group cohesion), localizability of signals would be

favored, whereas signaling in situations where advertising location is disadvantageous (e.g. presence of predators, aggressive rivals) should select for less locatable signals. Research in a variety of mammals, including some primates, indicates that calls are more localizable when their structure is more harsh (i.e. energy distributed widely across frequencies; "noisy"), frequency modulated, and repetitious (Terhune 1974; Brown et al. 1979; Lewis 1983). *Pyows* therefore may be the most localizable calls of the repertoire, given their high amplitude, sweeping frequency modulation, broadband structure, and tendency to be given in repeated bouts. *Ants*, *kas*, and *katrains* also share these characteristics, except for frequency modulation, though to a lesser degree. The *boom*, despite its considerable audible distance, is not frequency modulated, harsh, or typically repeated, and is thus likely one of the least localizable male vocalizations.

Lastly, some acoustic features can directly influence receivers by evoking reflexive neural responses (reviewed in Owren & Rendall 2001). The best understood example of this is the "acoustic-startle reflex," a phenomenon observed across mammals, birds, and anurans in which certain types of sounds trigger increased brain activity, shifts in attention, and other autonomic responses in receivers (reviewed in Eaton 1984). Sounds characterized by high amplitudes and short rises (i.e. time from signal onset to maximum amplitude) trigger this startle reflex, suggesting that selection favors use of signals with such structure when quickly shifting receivers' attention and arousal is beneficial (e.g. predator alarms, aggressive signals; Owren & Rendall 2001). The *ka*, *katrain*, and *ant* each have very short rise times relative to the *pyow* and the *boom* (Table 6). The startle reflex potential of *katrains* is likely magnified by the rapid repetition of individual units that each have high amplitude and short rise time.

Similarities to congeners

Acoustically, the calls of adult male blue monkeys are similar to signals of several close relatives. The *boom* is extremely similar to *booms* by other guenons, including *Cercopithecus nictitans*, *C. campbelli*, *C. neglectus*, *C. mona*, *C. pogonias*, *C. hamlyni*, and *C. lomamiensis* (Gautier, 1988; Bouchet et al. 2012; Hart et al. 2012), each of which relies on resonating an inflated laryngeal air sac to produce this signal (Gautier 1971; Hewitt et al. 2002). The *pyow* also bears a strong resemblance to the homonymous *pyow* by putty-nosed monkeys (*C. nictitans*; see Struhsaker 1970; Arnold & Zuberbühler 2006), the nearest congener of *C. mitis* (Disotell & Raum 2002). Putty-nosed monkeys also use a *hack* call that is structurally similar to *kas* (see Fig. 1 in Price et al. 2008; Gautier, 1988), though they do not appear to link them into multi-unit calls like the *katrain*. Given that primate vocal signals appear mainly genetically determined (Newman & Symes 1982), it is not surprising that such closely related species should have similar repertoires. Interestingly, however, the link between phylogenetic relatedness and sharing of call types is not consistent, with some call types more or less conserved among taxa and others more species specific. Male redtail monkeys (*Cercopithecus ascanius*) at the Kakamega Forest, for example, use signals remarkably similar to blue monkey *ants* and *katrains*, yet do not *boom* or *pyow* (unpublished data).

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Table 1. Sample size for analyzed recordings of different call types from different callers.

CALL TYPE	RECORDING SAMPLES	NUMBER OF MALES	SAMPLES PER MALE (range)	PERCENTAGE OF ALL RECORDED CALLS
ANT	66	9	3 – 10	9%
BOOM	211	16	4 – 29	27%
KA	28	7	2 – 6	4%
KATRAIN	39	8	1 – 9	5%
NASAL SCREAM	11	4	1 – 5	1%
PYOW	417	19	8 – 62	54%

Table 2. Parameters used to examine acoustic structure of vocal signals. The extension ".tot" on parameter names refers to measurements of the total call.

	PARAMETER	UNITS	DESCRIPTION
1	**Cent_frq**	Hertz (Hz)	The frequency dividing call into two frequency intervals of equal energy.
2	**Low_Frq_tot**	Hz	Call's lower frequency limit.
3	**Hi_Frq_tot**	Hz	Call's upper frequency limit (assessed only in *boom* and individual frequency bands measured in parameters 16-43).
4	**Max_Frq_tot**	Hz	Frequency at which maximum power (amplitude) occurs. If occurred at more than one time / frequency bin, Max_Frq is lowest frequency at first time max power occurred.
5	**Delta_Frq_tot**	Hz	Frequency range in which energy above ambient noise was detectable (i.e. difference between call's upper and lower frequency limits).
6	**Delt_time_tot**	Seconds (sec)	Call's duration, i.e. the time period during which energy (not including echo) was perceptible in the amplitude waveform.
7	**Start_Frq_tot**	Hz	Maximum frequency (see 4, Max_Frq) during first 25% of call
8	**Mid_Frq_tot**	Hz	The maximum frequency (see 4, Max_Frq) during middle 25% of call
9	**End_Frq_tot**	Hz	Maximum frequency (see 4, Max_Frq) during last 25% of call.
10	**Slope_tot**	Hz per sec	The slope, or rate of frequency change, from call's start to its end; i.e. (Start_Frq – End_Frq) / Delt_time.
11	**Slope_1st_tot**	Hz per sec	The slope, or rate of frequency change, from call's start to its midpoint; i.e. (Start_Frq – Mid_Frq) / (Delt_time x 0.5)
12	**Slope_2nd_tot**	Hz per sec	The slope, or rate of frequency change, from call's midpoint to its end; i.e. (Mid_Frq – End_Frq) / (Delt_time x 0.5)
13	**Rise_abs_tot**	Sec	The rise of the call; i.e. interval from call's start to the time at which maximum power (peak amplitude) first occurs.
14	**Rise_rel_tot**	Proportion	The rise of call (see 13, above) divided by call's duration.
15	**Rise_slope_tot**	Hz per sec	The slope, or rate of frequency change, during call's rise; difference between Start_Frq and Max_Frq divided by Rise_abs.
16-30	**Same measures described in Parameters 1-15 applied to call's fundamental frequency band (F0).** Parameter names are same as above, with extension "_F0" instead of "_tot."		
30-45	**Same measures in Parameters 1-15 applied to first dominant frequency band (DF1).**		
46	**Formant_disp_1**	Hz	The mean difference between frequency peaks of the first dominant band (DF1) and the fundamental band (F0).
47	**Formant_disp_2**	Hz	The mean difference between frequency peaks of the second dominant band (DF2) and the first dominant band (DF1).
48	**Formant_disp_mean**	Hz	Average distance between formants: $1/n \sum_{i=1}^{n}(\text{FDisp\_1-2}_i)$
49	**Number_units**	Discrete units	Number of temporally discrete acoustic pulses (i.e. "syllables" separated by detectable silence). Relevant to *katrains* only.
50	**Inter-unit_intrvl**	Sec	Interval between beginning of discrete unit (see 49) and end of previous unit. Note: only relevant to *katrains*.

Table 3. Proportion of variance contained in the first three principal components. For each PC, acoustic variables are ranked according to highest factor loading values for qualitative assessment of variables that best describe variance among call samples.

	PC1		PC2		PC3		PC4		PC5	
Proportion of Variance Explained	0.453		0.161		0.109		0.059		0.052	
Cumulative Proportion of Variance Explained	0.453		0.614		0.723		0.782		0.833	
Loading Variables	Mean.frmt.disp	12%	Rise_abs_Fo	29%	Slope_tot	41%	Rise_rel_Fo	55%	Rise_rel_tot	46%
	Slope_2_F1	10%	Dur_tot	22%	Slope_1_tot	39%	Dur_tot	19%	Slope_1_tot	18%
	Cent_frq	10%	Rise_rel_Fo	14%	Start_frq_tot	12%	Max_frq_Fo	13%	Slope_tot	8%
	Delta_frq_Fo	10%	Low_frq_Fo	8%	Slope_2_Fo	2%	Rise_rel_tot	5%	Slope_2_Fo	6%
	Max_frq_Fo	10%	Rise_rel_tot	7%	Rise_rel_tot	1%	Slope_2_Fo	3%	Rise_rel_Fo	6%
	Slope_Fo	9%	Slope_1_F1	4%	Rise_rel_Fo	1%	Slope_2_F1	1%	Cent_frq	5%
	Low_frq_Fo	8%	Slope_Fo	3%	Slope_2_F1	1%	Slope_Fo	1%	Dur_tot	3%
	Slope_1_F1	8%	Cent_frq	2%	Mean.frmt.disp	1%	Delta_frq_Fo	1%	Start_frq_tot	3%
	Start_frq_tot	8%	Start_frq_tot	2%	Rise_abs_Fo	1%	Slope_1_tot	1%	Rise_abs_Fo	2%
	Slope_2_Fo	8%	Max_frq_Fo	2%	Max_frq_Fo	<1%	Mean.frmt.disp	1%	Max_frq_Fo	1%
	Rise_rel_tot	3%	Slope_2_F1	2%	Low_frq_Fo	<1%	Slope_tot	<1%	Low_frq_Fo	1%
	Rise_abs_Fo	2%	Mean.frmt.disp	2%	Slope_1_F1	<1%	Cent_frq	<1%	Mean.frmt.disp	<1%
	Dur_tot	1%	Slope_2_Fo	2%	Slope_Fo	<1%	Low_frq_Fo	<1%	Slope_2_F1	<1%
	Slope_tot	<1%	Slope_1_tot	1%	Delta_frq_Fo	<1%	Slope_1_F1	<1%	Delta_frq_Fo	<1%
	Slope_1_tot	<1%	Delta_frq_Fo	<1%	Dur_tot	<1%	Rise_abs_Fo	<1%	Slope_Fo	<1%
	Rise_rel_Fo	<1%	Slope_tot	<1%	Cent_frq	<1%	Start_frq_tot	<1%	Slope_1_F1	<1%

Table 4. Proportion of samples assigned correctly to each call type in discriminant function analysis. Probability that a sample would be assigned correctly by chance was 0.167. For each call type, proportions and targets of incorrect classifications are listed.

	ANT	BOOM	KA	KATRAIN (units)	NASAL SCREAM	PYOW	ALL
Proportion assigned correctly	0.69	1.00	0.46	0.77	1.00	0.85	0.795
Proportion assigned incorrectly as:	Ka: 0.15 Katrain: 0.12 Pyow: 0.04	None	Katrain: 0.46 Ant: 0.04 Pyow 0.04	Ka: 0.23	None	Ant: 0.11 Ka: 0.04	

Table 5. Proportion of variance explained by the first three linear discriminant functions (LD). Acoustic variables with the greatest coefficients for each LD are listed for a qualitative assessment of variables that best describe variance among call samples.

	LD1	LD2	LD3
Proportion of Variance Explained	0.548	0.366	0.063
Cumulative Proportion of Variance Explained	0.548	0.914	0.978
Highest Coefficient Variables	Dur_tot: 77% Rise_abs_F0: 17%	Rise_abs_F0: 55% Dur_tot: 31%	Dur_tot: 93% Rise_rel_F0: 5%

Table 6. Summary of measurements (mean ± SE) of the acoustic structure of each call type. Sample sizes for each call type refer to the number of males whose recordings were sampled. The acoustic parameters listed are a subset of those described in Table 2.

CALL TYPE	Units	Cent_frq	Dur_ tot	Start_frq_ tot	Slope_ tot	Slope_1_ tot	Rise_rel_ tot	Low_frq_ Fo	Max_frq_ Fo	Delta_frq Fo
ANT (n=9)	1 ± 0	1620.39 ± 121.98	0.04 ± 0.01	1387.29 ± 186.08	-2034.51 ± 5254.27	3092.86 ± 4455.18	0.52 ± 0.07	154.02 ± 8.37	295.32 ± 19.65	277.18 ± 19.82
BOOM (n=16)	1 ± 0	123.97 ± 1.69	0.13 ± 0	129.6 ± 1.26	-103.02 ± 14.97	10.52 ± 10.52	0.39 ± 0.01	68.58 ± 1.78	130.26 ± 1.06	117.48 ± 2.02
KA (n=7)	1 ± 0	856.38 ± 35.25	0.06 ± 0	851.77 ± 54.9	221.41 ± 461.59	-1217.46 ± 1073.79	0.54 ± 0.05	161.41 ± 6.66	324.28 ± 32	297.53 ± 23.42
KATRAIN (units) (n=8)	1 ± 0	861.34 ± 22.93	0.05 ± 0	867.68 ± 29.86	-299.36 ± 320.44	-202.22 ± 800.5	0.53 ± 0.03	155.54 ± 4.72	277.82 ± 12	255.49 ± 6.59
KATRAIN (call) (n=8)	15.94 ± 1.02	833.26 ± 10.85	4.23 ± 0.22	872.34 ± 16	-10 ± 4.2	-4.76 ± 8.59	0.44 ± 0.05	n/a	n/a	n/a
NASAL SCREAM (n=4)	1 ± 0	1396.62 ± 495.01	0.44 ± 0.09	1279.1 ± 518.88	171.87 ± 23	-840.03 ± 1349.02	0.7 ± 0.07	234.37 ± 25.63	385.4 ± 45.89	205.53 ± 23.85
PYOW (n=19)	1 ± 0	1590.12 ± 48.54	0.1 ± 0	1652.36 ± 120.45	-3175.15 ± 1234.53	-890.38 ± 2164.9	0.62 ± 0.02	194.94 ± 5.46	366.5 ± 9.71	400.08 ± 18.4

(Table 6, cont.)

CALL TYPE	Slope_Fo	Slope_2_Fo	Rise_abs_Fo	Rise_rel_Fo	Slope_1_F1	Slope_2_F1	Mean_frmt_disp
ANT (n=9)	-2836.7 ± 223.6	-2327.69 ± 232.47	0.01 ± 0	0.31 ± 0.07	-4502.59 ± 615.79	-4437.98 ± 382.31	257.63 ± 12.51
BOOM (n=16)	-103.92 ± 15.1	-218.36 ± 29.78	0.05 ± 0	0.39 ± 0.01	n/a	n/a	n/a
KA (n=7)	-3259.35 ± 497.3	-1091.25 ± 313.47	0.02 ± 0	0.34 ± 0.06	-5172.47 ± 716.58	-3786.44 ± 638.33	261.34 ± 6.8
KATRAIN (units) (n=8)	-3668.93 ± 241.75	-2298.68 ± 188.48	0.02 ± 0	0.38 ± 0.03	-4478.84 ± 570.13	-4431.07 ± 227.18	233.93 ± 5.01
KATRAIN (call) (n=8)	n/a	n/a	n/a	n/a	n/a	n/a	n/a
NASAL SCREAM (n=4)	68.05 ± 82.9	-298.61 ± 111.21	0.2 ± 0.04	0.64 ± 0.14	621.83 ± 221.48	-178.7 ± 103.22	239.67 ± 23.67
PYOW (n=19)	-2457.51 ± 208.99	-1977.48 ± 159.43	0.04 ± 0	0.43 ± 0.02	-3372.31 ± 271.02	-3875.96 ± 246.12	344.04 ± 5.88

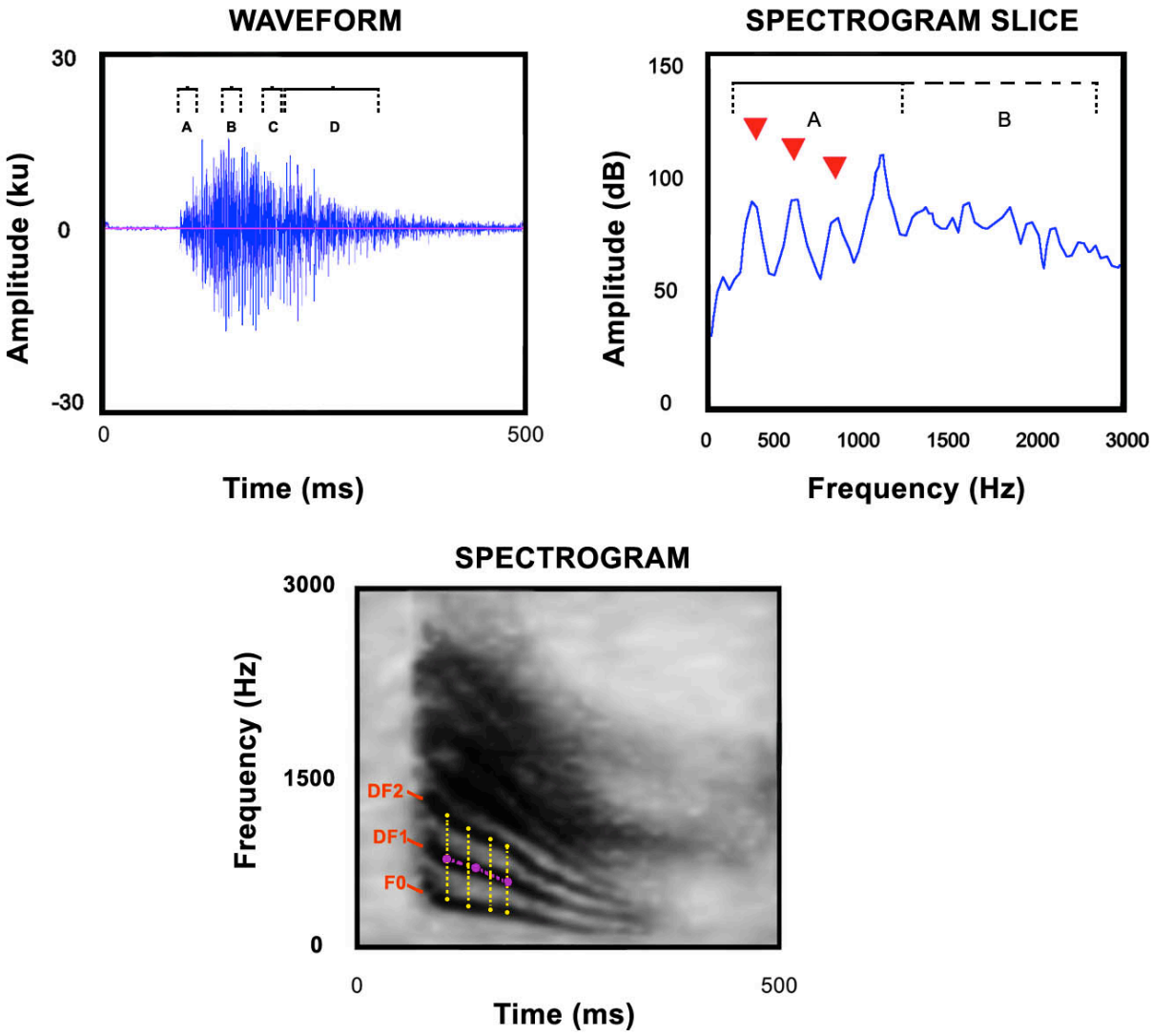

Figure 1. Exemplar graphs of a *pyow*, illustrating how acoustic measures were obtained.

Top, left: Power-time oscillogram (waveform). Y-axis shows amplitude (energy), X-axis shows time. A, B, and C indicate first, middle, and last quartiles of the call, respectively. D indicates echo of source signal and decay as call energy dissipates to ambient level.

Top, right: Frequency-power spectrum (spectrogram slice). Y-axis is amplitude (acoustic energy) and X-axis is frequency. Triangles indicate the first three dominant frequency bands (F0, DF1, and DF2). Energy concentrated in frequency peaks (A) versus dispersed across frequencies (B) characterize degree to which call is tonal or noisy.

Middle: Spectrogram. Y-axis shows frequency, X-axis shows time in milliseconds, and variation in saturation from white to black reflects amplitude (acoustic energy). F0, DF1, and DF2 are the first three dominant frequency bands. Yellow dots are peak frequencies on different bands at different times, from which frequency dispersion between bands (yellow dotted lines) was calculated. Purple dots are peak frequencies at the start, middle, and end of the DF1, from which slopes (purple dotted line) were calculated.

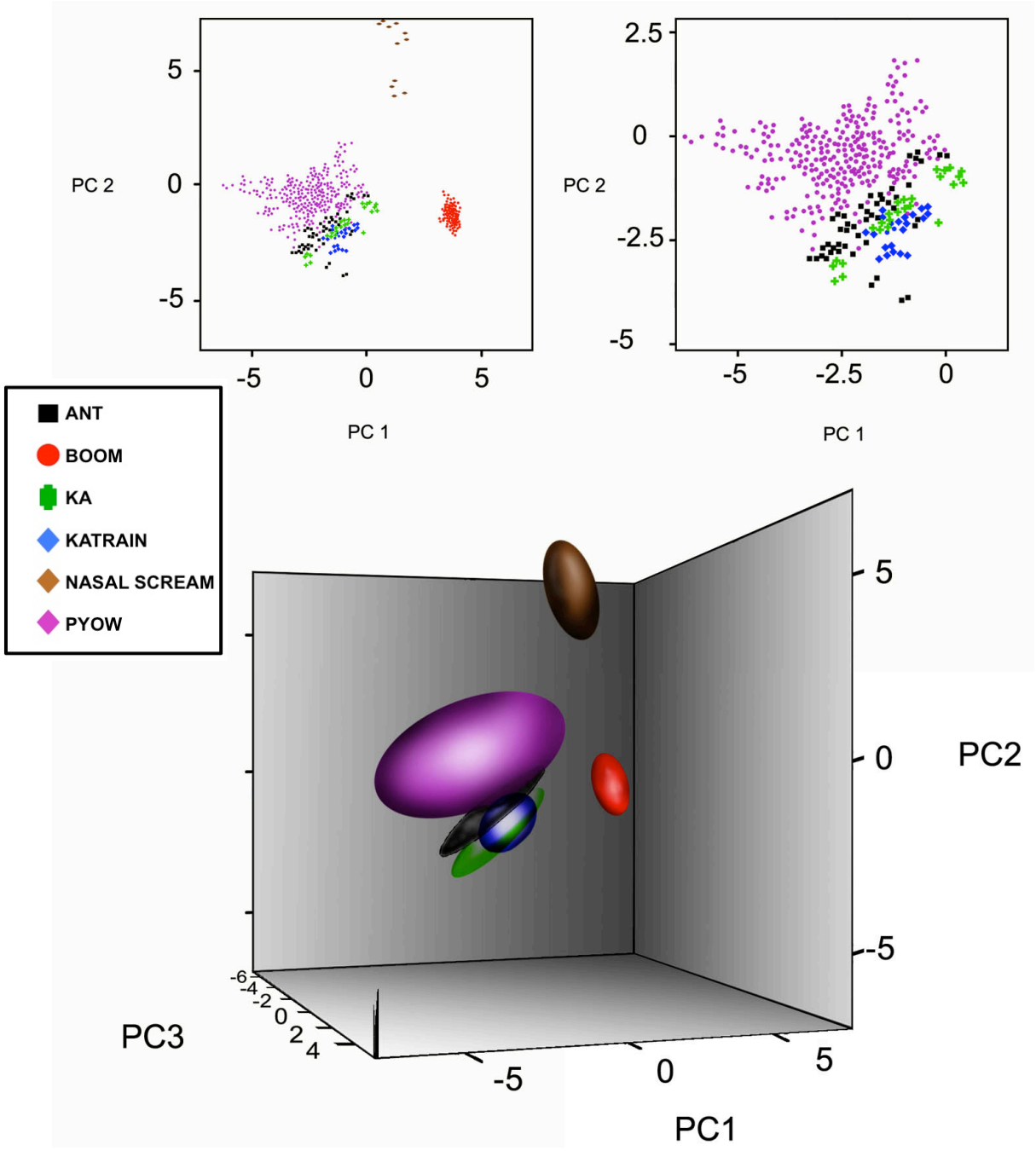

Figure 2. Call samples (n= 772) plotted in space defined by principal components.

Top, left: All call samples plotted along PC1 and PC2. Note the distinct clusters of *booms* and *nasal screams*, and the convergent cluster of *pyows*, *ants*, *kas*, and *katrains*.

Top, right: The same plot, zoomed to exclude *booms* and *nasal screams* and emphasize relationships among *pyows*, *ants*, *kas*, and *katrains*.

Bottom: All call samples plotted in three-dimensional space along PC1, PC2, and PC3.

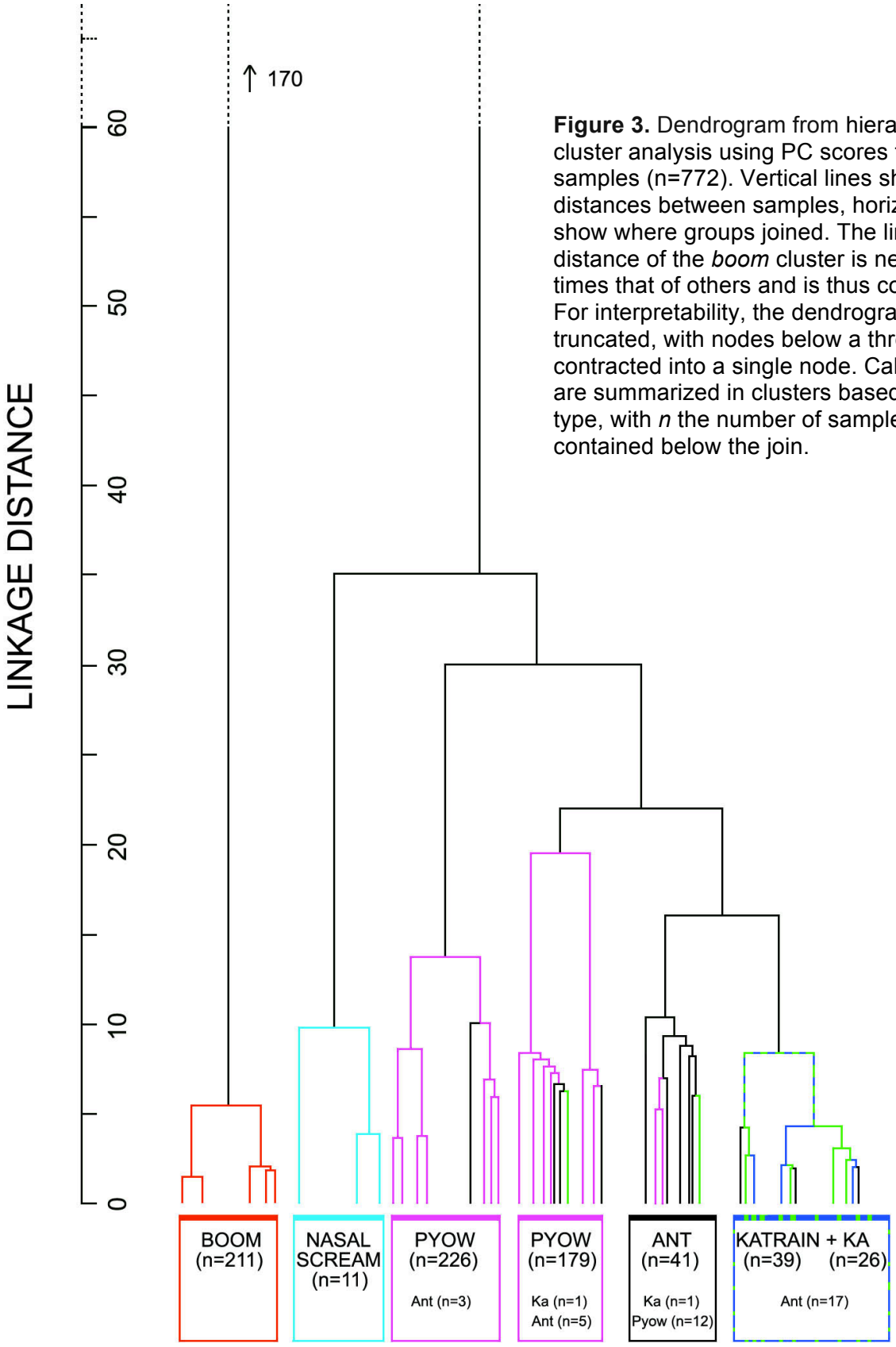

Figure 3. Dendrogram from hierarchical cluster analysis using PC scores for all call samples (n=772). Vertical lines show distances between samples, horizontal lines show where groups joined. The linkage distance of the *boom* cluster is nearly seven times that of others and is thus condensed. For interpretability, the dendrogram is truncated, with nodes below a threshold 2.0 contracted into a single node. Call samples are summarized in clusters based on call type, with *n* the number of samples contained below the join.

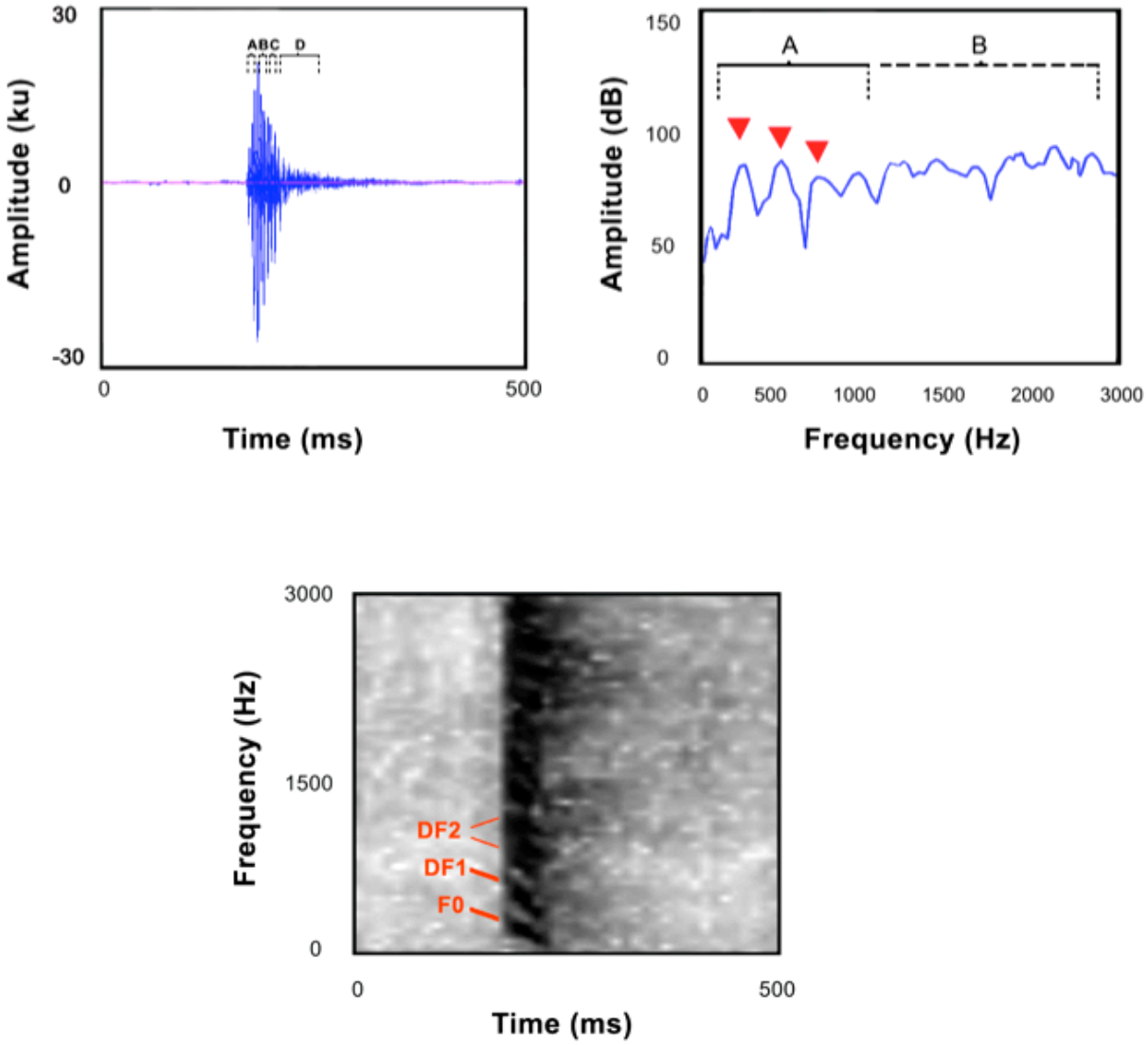

Figure 4. Exemplar graphs of the acoustic structure of the *ant*.

Top, left: Power-time oscillogram (waveform). Y-axis shows amplitude (acoustic energy) and X-axis shows time. A, B, and C indicate the first, middle, and last quartiles of call, respectively. D indicates echo decay as call energy dissipates to ambient level.

Top, right: Frequency-power spectrum (spectrogram slice). Y-axis shows amplitude (acoustic energy), X-axis shows frequency. Triangles indicate the first three dominant frequency bands (F0, DF1, DF2). A indicates the tonal portion of the call (energy concentrated in distinct frequency peaks), B indicates the noisy portion (energy dispersed across frequencies).

Bottom: Spectrogram. Y-axis shows frequency, X-axis shows time, and saturation from white to black reflects amplitude (acoustic energy). F0, DF1, and DF2 indicate the first three dominant frequency bands. The third band (DF2) was variably discernible in recordings, with most recordings indicating only a dense cluster of energy near 900 Hz.

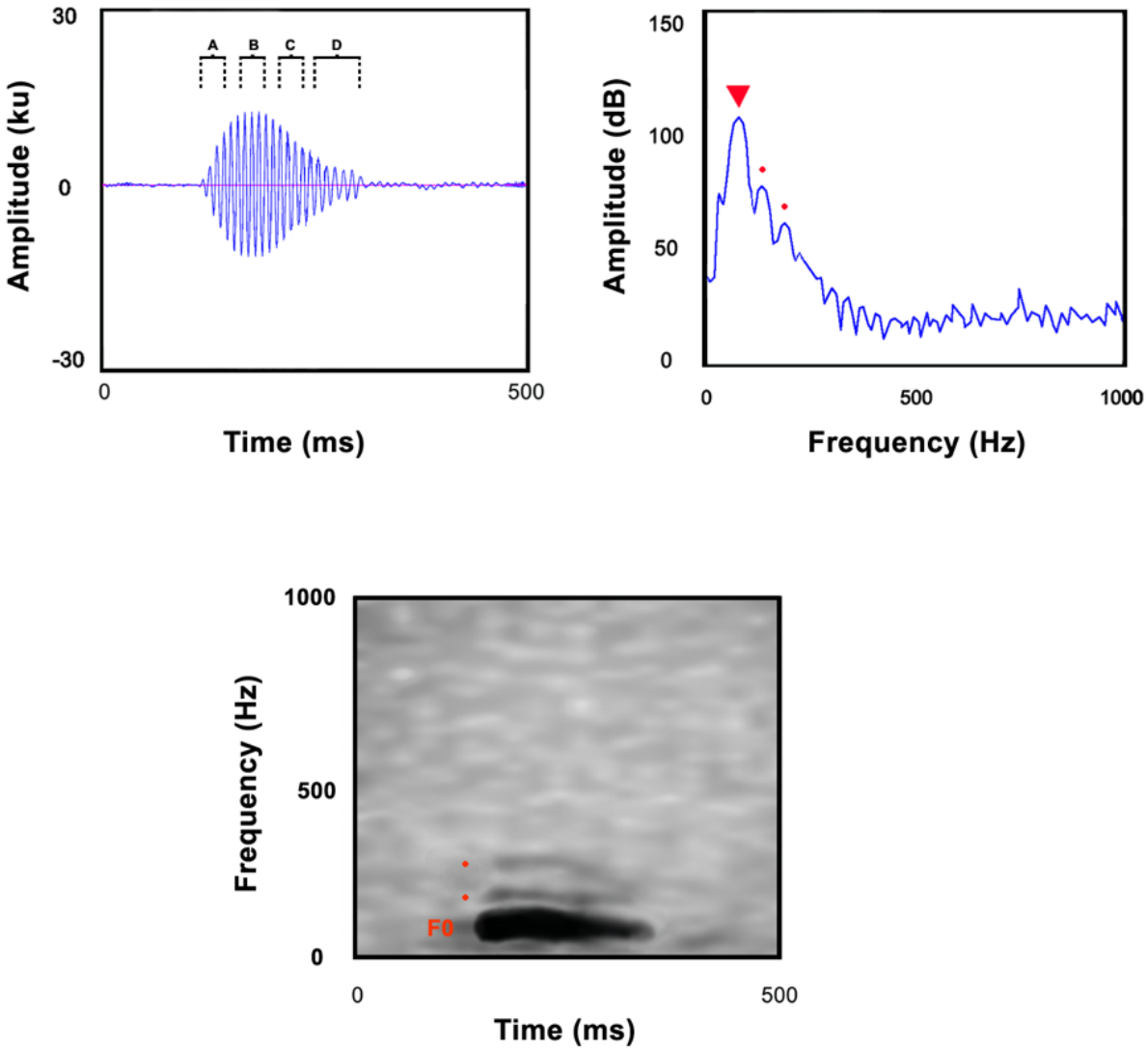

Figure 5. Exemplar graphs of the acoustic structure of the *boom*.

Top, left: Power-time oscillogram (waveform view). Y-axis shows amplitude (acoustic energy) and X-axis shows time. A, B, and C indicate the first, middle, and last quartiles of call, respectively. D indicates echo decay as call energy dissipates to ambient level.

Top, right: Frequency-power spectrum (spectrogram slice). Y-axis shows amplitude (acoustic energy) and X-axis shows frequency. The triangle indicates the fundamental frequency band (F0), which in the boom constitutes the entire call, and the two red circles indicate harmonics that can be detected only in some recordings.

Bottom: Spectrogram. Y-axis shows frequency, X-axis shows time, and saturation from white to black reflects amplitude (acoustic energy). Note that, unlike other call types, there is only one dominant frequency band (F0), though one to two harmonics were discernible in a few recordings.

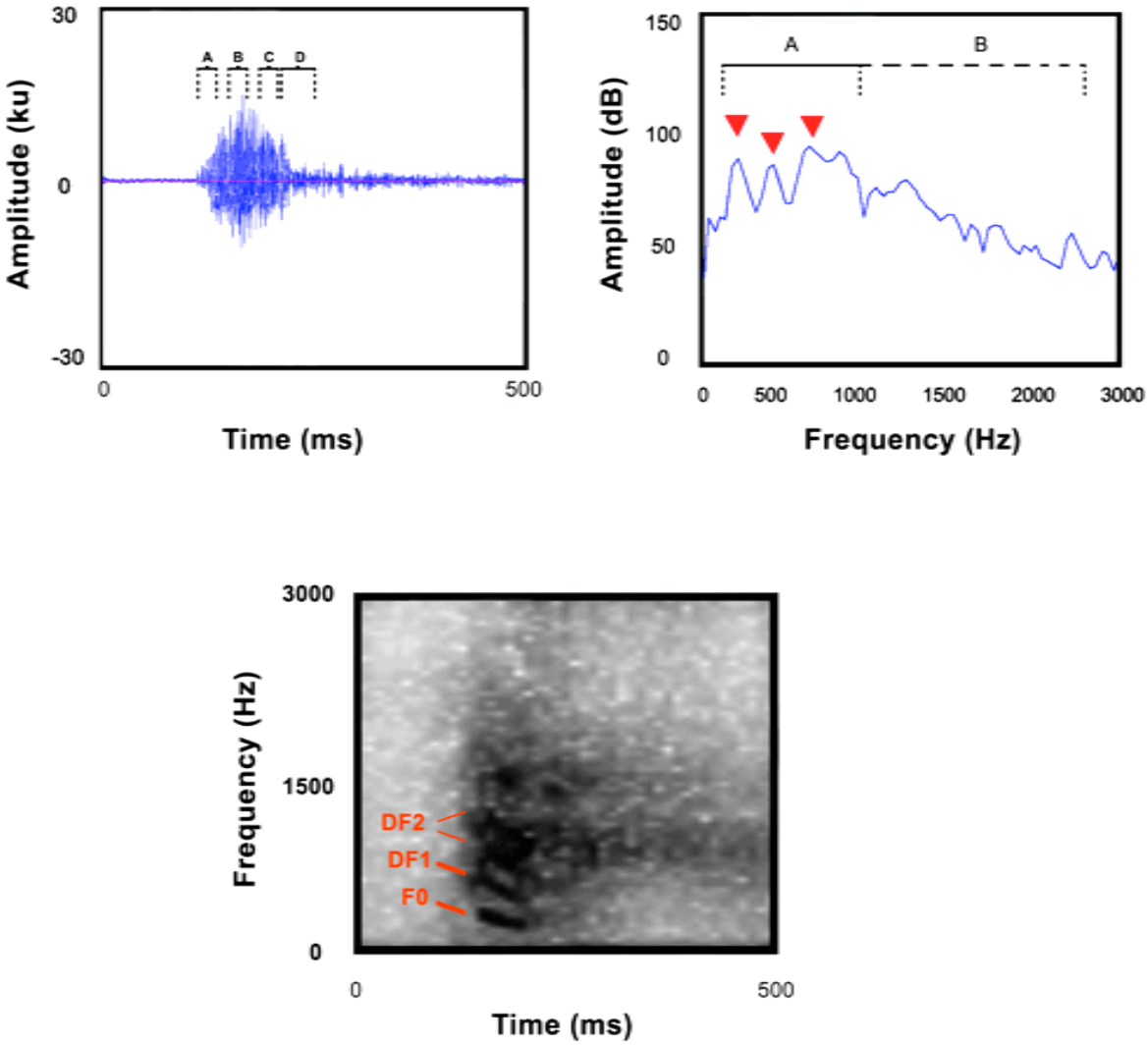

Figure 6. Exemplar graphs of the acoustic structure of the *ka*.

Top, left: Power-time oscillogram (waveform). Y-axis shows amplitude (acoustic energy) and X-axis shows time. A, B, and C indicate the first, middle, and last quartiles of call, respectively. D indicates echo decay as call energy dissipates to ambient level.

Top, right: Frequency-power spectrum (spectrogram slice). Y-axis shows amplitude (acoustic energy) and X-axis shows frequency. Triangles indicate the first three dominant frequency bands (F0, DF1, and DF2). A indicates the tonal portion of the call (energy concentrated in distinct frequency peaks), and B indicates the noisy portion (energy dispersed across frequencies).

Bottom: Spectrogram. Y-axis shows frequency, X-axis shows time, and saturation from white to black reflects amplitude (acoustic energy). F0, DF1, and DF2 indicate first three dominant frequency bands. Similar to the *ant*, the third band (DF2) of the *ka* was variably discernible in recordings, with most indicating only a cluster of energy near 900 Hz.

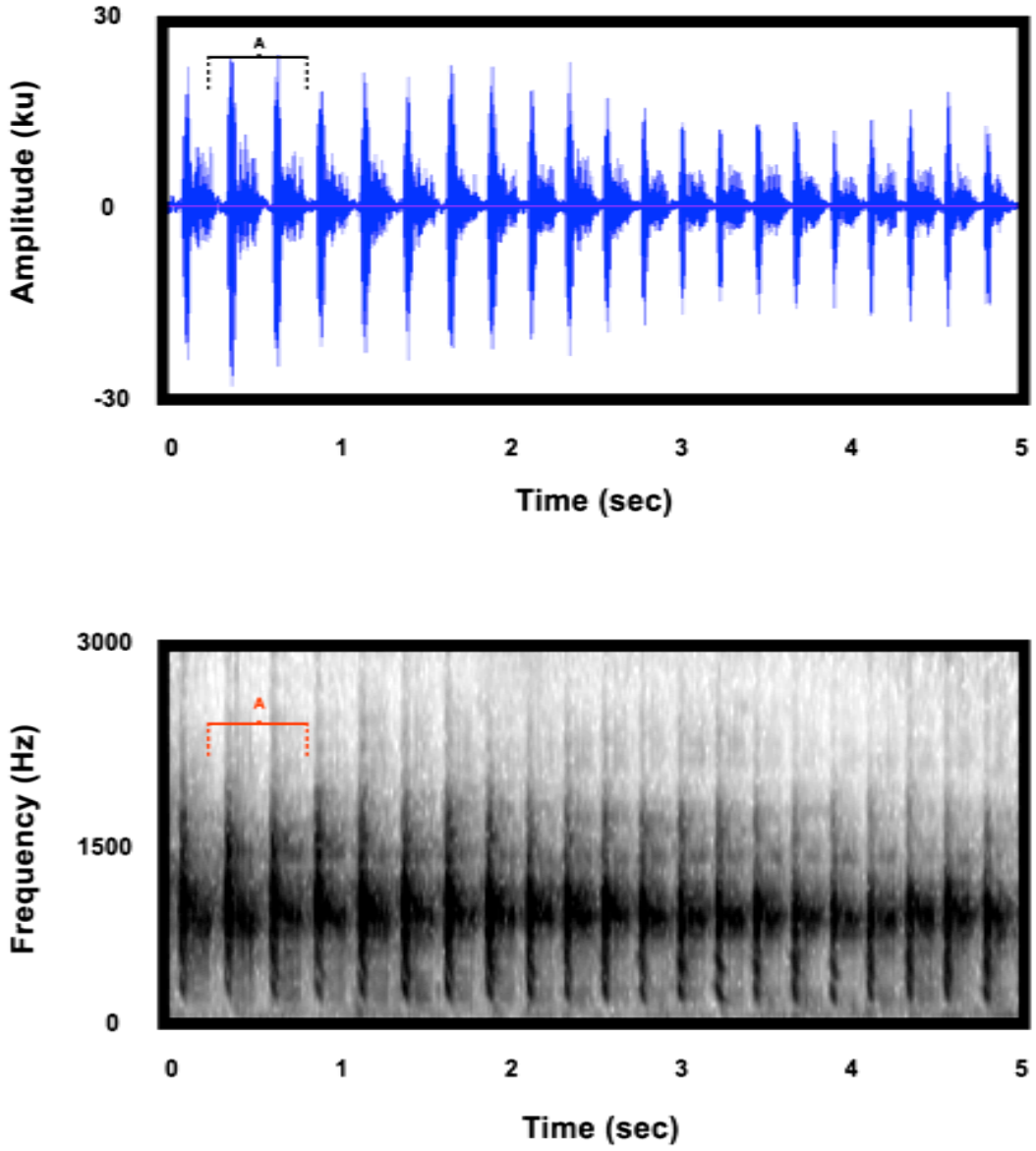

Figure 7. Exemplar graphs of the acoustic structure of the *katrain*. To illustrate the call's multi-unit structure, separate graphs are provided for the entire call (shown here, with 21 individual units) and the individual units within the call (Figure 8).

Top: Power-time oscillogram (waveform). Y-axis shows amplitude (acoustic energy) and X-axis shows time. A indicates two units within the train, also shown in Figure 8.

Bottom: Spectrogram. Y-axis shows frequency, X-axis shows time, and saturation from white to black reflects amplitude (acoustic energy). A indicates the two consecutive units in the call shown in Figure 8.

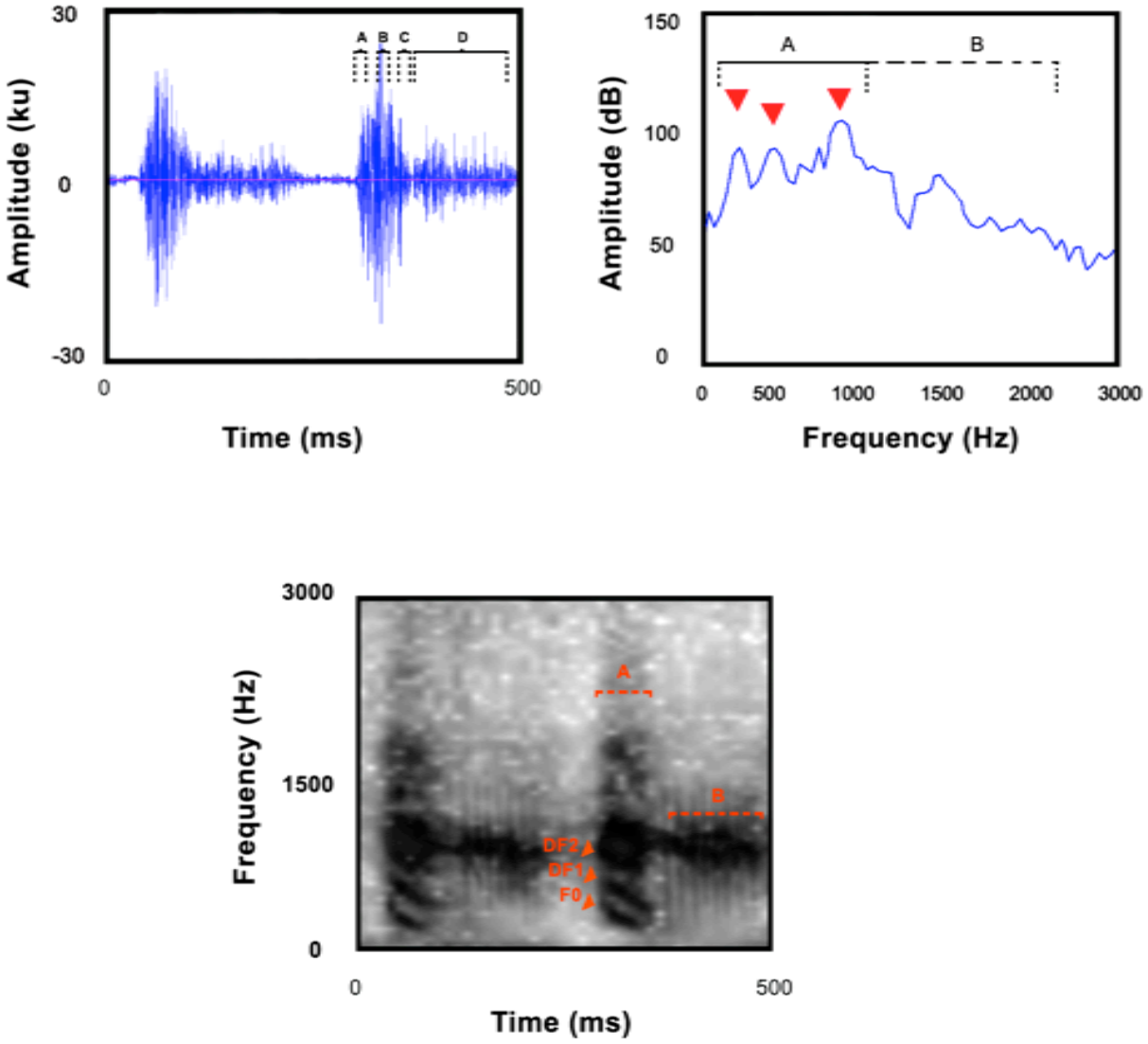

Figure 8. Two consecutive units within a *katrain*.

Top, left: Power-time oscillogram (waveform). Y-axis shows amplitude (acoustic energy) and X-axis shows time. A, B, and C indicate the first, middle, and last quartiles of one unit, respectively. D indicates the "*urrr*" sound that separates units.

Top, right: Frequency-power spectrum (spectrogram slice) of one unit. Y-axis shows amplitude (acoustic energy) and X-axis shows frequency. Triangles indicate the first three dominant frequency bands (F0, DF1, and DF2). A indicates the tonal portion of the call (energy concentrated in distinct frequency peaks), and B indicates the noisy portion (energy dispersed across frequencies).

Bottom: Spectrogram. Y-axis shows frequency, X-axis shows time, and saturation from white to black reflects amplitude (acoustic energy). A indicates a single unit and B indicates the "*urrr*" that separates units. F0, DF1, and DF2 indicate the first three dominant frequency bands.

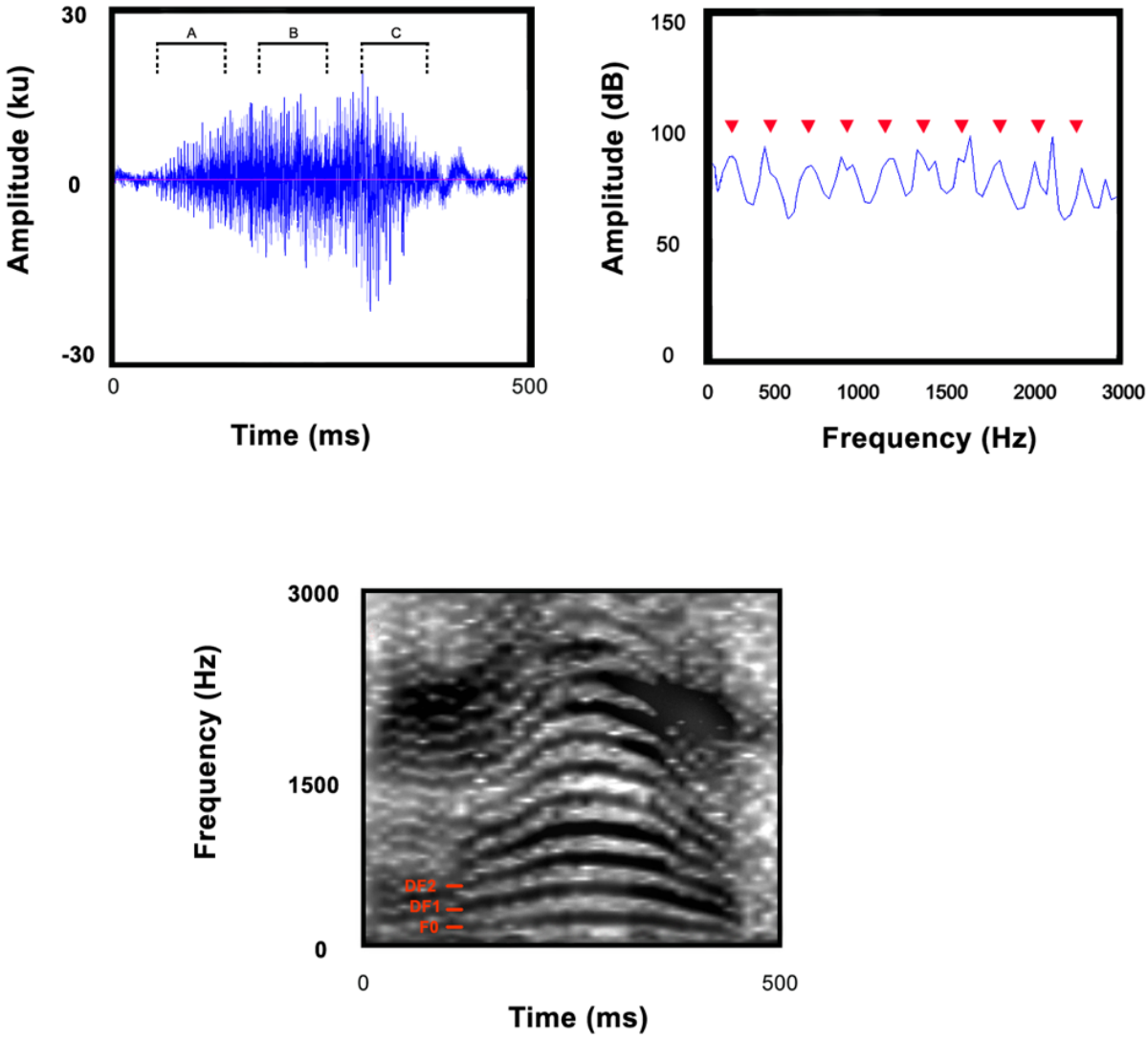

Figure 9. Exemplar graphs of the acoustic structure of the *nasal scream*.

Top, left: Power-time oscillogram (waveform). Y-axis shows amplitude (acoustic energy) and X-axis shows time. A, B, and C indicate the first, middle, and last quartiles of the call, respectively.

Top, right: Frequency-power spectrum (spectrogram slice). Y-axis shows amplitude (acoustic energy) and X-axis shows frequency. Triangles indicate dominant frequency bands, reflecting energy concentrated in distinct peaks throughout frequency range.

Middle: Spectrogram. Y-axis shows frequency, X-axis shows time, and saturation from white to black reflects amplitude (acoustic energy). F0, DF1, and DF2 indicate the first three dominant frequency bands.

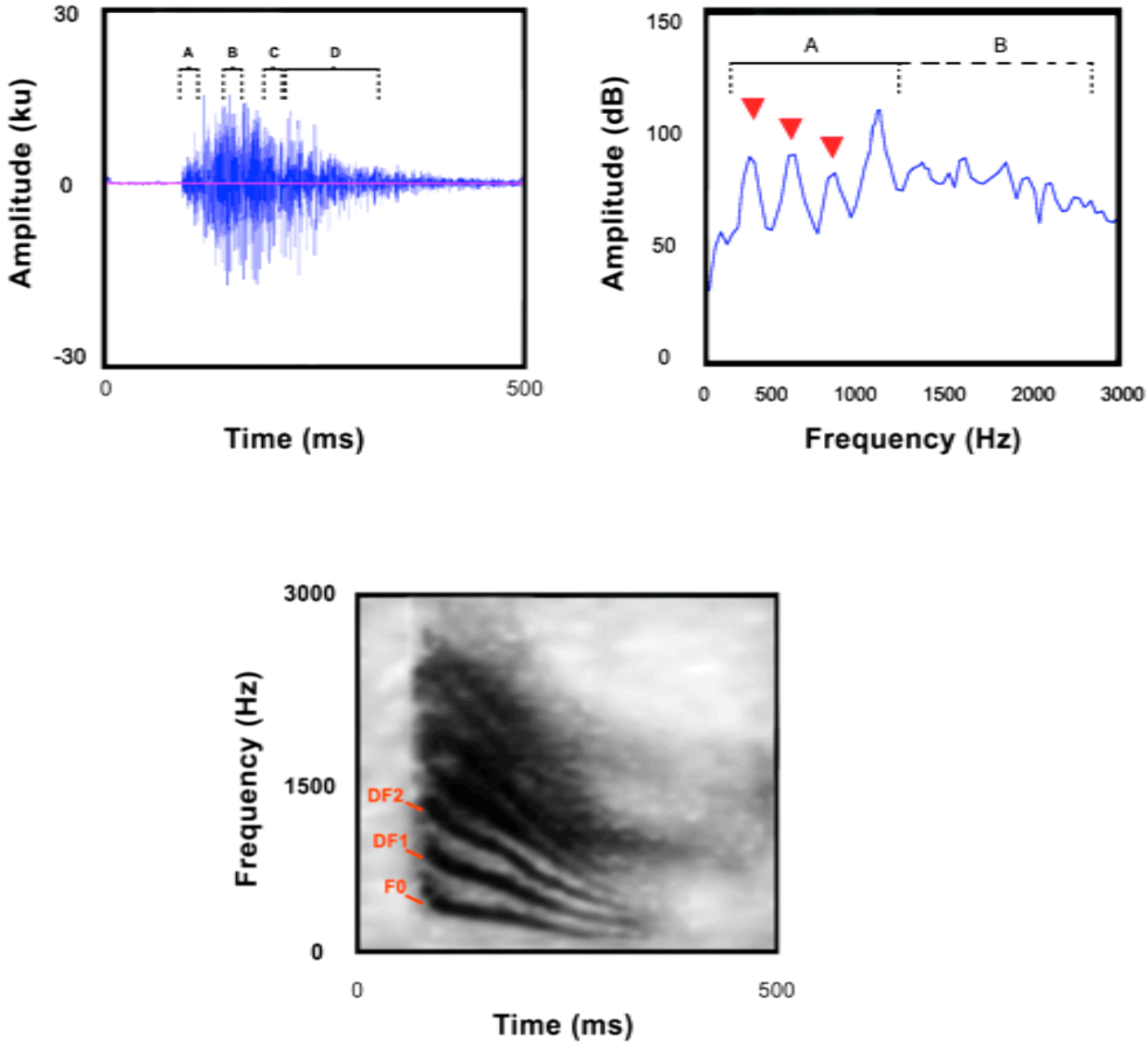

Figure 10. Exemplar graphs of the acoustic structure of the *pyow*.

Top, left: Power-time oscillogram (waveform). Y-axis shows amplitude (acoustic energy) and X-axis shows time. A, B, and C indicate the first, middle, and last quartiles of the call, respectively. D indicates echo decay as call energy dissipates to ambient level.

Top, right: Frequency-power spectrum (spectrogram slice). Y-axis shows amplitude (acoustic energy) and X-axis shows frequency. Triangles indicate first three dominant frequency bands (F0, DF1, DF2). A indicates the tonal portion of call (energy concentrated in distinct frequency peaks), and B indicates noisy portion (energy dispersed across frequencies).

Bottom: Spectrogram. Y-axis shows frequency, X-axis shows time, and saturation from white to black reflects amplitude (acoustic energy). F0, DF1, and DF2 indicate the first three dominant frequency bands.

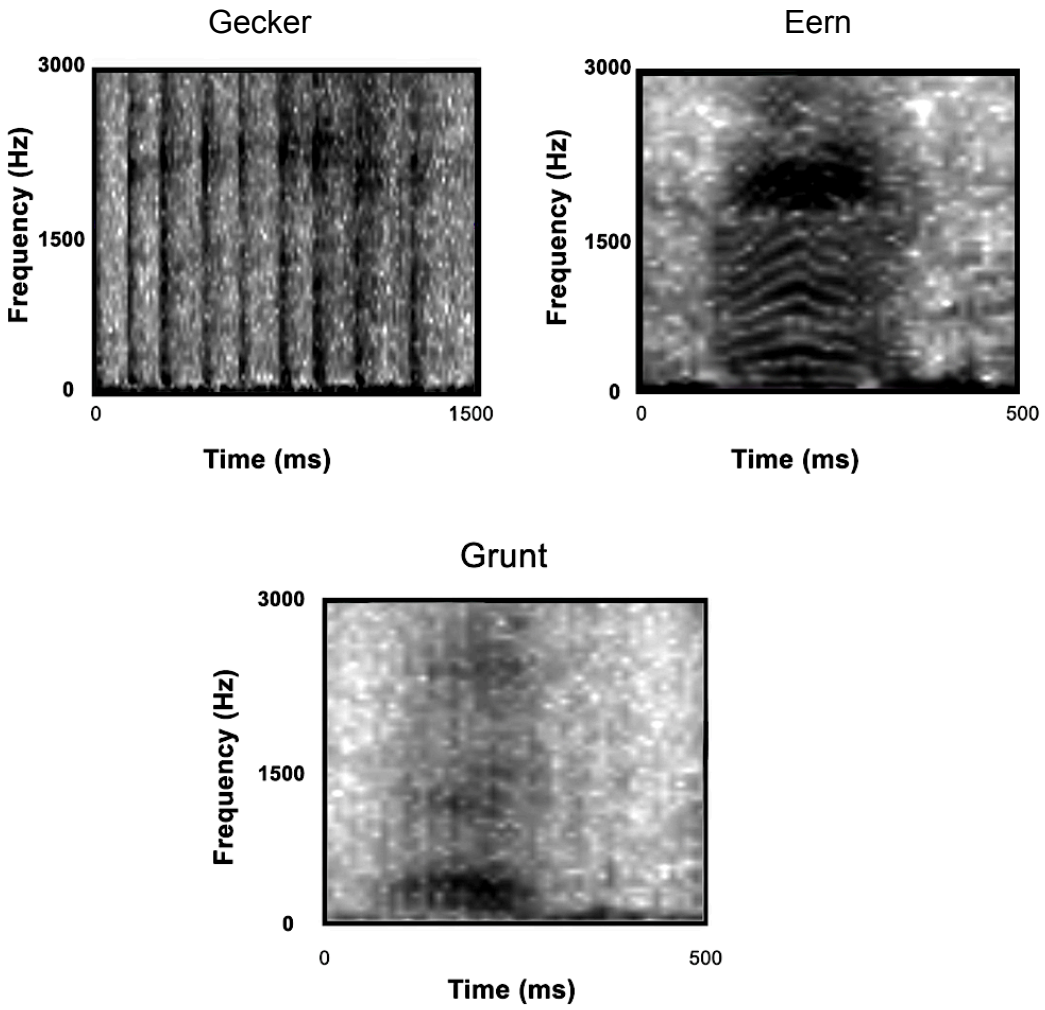

Figure 11. Exemplar spectrograms of the *Gecker*, *Eern*, and *Grunt*. Y-axis shows frequency, X-axis shows time, and saturation from white to black reflects amplitude (acoustic energy). Note that the spectrogram for the *gecker* (top, left) comprises a longer time window.

CHAPTER 3

SIGNAL CONTENT IN THE VOCAL REPERTOIRE OF ADULT MALE BLUE MONKEYS (*CERCOPITHECUS MITIS STUHLMANNI*): CALL FEATURES AS RELIABLE INDICATORS OF CALLER ATTRIBUTES.

ABSTRACT

From an evolutionary perspective, animal signals are favored by selection because they evoke responses by receivers that benefit signalers. Receivers are also subject to selection, and should respond according to their own fitness priorities, thereby favoring signals that have adaptive relevance to receivers. Identifying *signal content* – attributes of signalers that are reliably indicated by features of signals – and how it relates to receiver responses is therefore critical to understanding how signals operate and evolve. During 12 months in the Kakamega Forest, Kenya, I examined vocal behavior of 32 adult male blue monkeys (*C. m. stuhlmanni*) to identify content in each of the six call types in the male repertoire. I investigated whether call types were reliable indicators of identity, social status, body size, and attention to external variables (e.g. predators), using data from > 4,000 hours of natural observations, 84 experimental stimulus trials (simulating predators or "intruder" males), and acoustic analysis of recorded calls. Results showed at least three call types (*boom*, *katrain*, *pyow*) were reliable indicators of identity, and features of at least one call type (*pyow*) were correlated with body size. Five calls were

used by resident males and never by "bachelors," indicating social status is content in all calls except *nasal screams*. Two call types (*ka*, *katrain*) were strongly associated with and essentially exclusive to aerial predators, and one call (*ant*) had a similar relationship to terrestrial predators. A fourth call (*pyow*) was strongly associated with terrestrial predators as well as presence of other males, and frequently used with no observable stimuli (i.e. "spontaneous"), and a fifth call (*boom*) was similarly associated with multiple external variables, appearing to function in male-female interactions; the lack of exclusivity demonstrates that content for these two calls does not include any specific external stimulus. Lastly, the content of *nasal screams*, used exclusively during aggression with other males, included presence of another male. I discuss the potential mechanisms by which signal honesty could be maintained, as well as functional implications for the different call types in this repertoire.

INTRODUCTION

From an evolutionary perspective, signals used in animal communication should reflect selection favoring behaviors that benefit signalers, with said benefit derived from a signal's ability to evoke responses by receivers (Wilson 1975; Dawkins & Krebs 1978; Blumberg & Alberts 1997; Dawkins & Guilford 1997). Receiver responses, as the principal function (*sensu* Tinbergen 1963) of signals, are thus central to understanding the evolution of communication and have accordingly received substantial research attention (reviewed in Hauser 1996; Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003). Signals, however, are unlikely to evolve solely under unidirectional

selection favoring manipulation of receivers. Receivers, also under selection, should respond to signals according to their own fitness priorities, thereby fostering selection for signals that are of adaptive relevance to receivers (Krebs & Dawkins 1984; Krebs & Davies 1993; Maynard Smith & Harper 2003). For example, in some frog species, males move away from low-pitch calls by other males (e.g. Robertson 1986), even when they have not seen the caller and despite the sound itself being harmless. Though signalers clearly benefit by repelling competitors, retreating receivers acquire little benefit (and indeed, energetic and opportunity costs), and are thus unlikely to have evolved such a response, unless the call is associated with something relevant to them. In the case of anuran vocalizations, fundamental frequency is correlated with body size, which relates to fighting ability (reviewed in Gerhardt & Huber 2002), providing explanation for how receiver response is adaptive for both signaler and receiver.

Though researchers continue to debate mechanisms by which some signals operate (e.g. by triggering reflexive responses, reviewed in Owren & Rendall 2001; or more complex cognitive processing and assessment, reviewed in Seyfarth et al. 2010), the evolutionary explanation should be the same: for selection to favor receivers responding in a consistent fashion, a signal must relate to something relevant to receivers. Identifying how signals relate to the fitness of receivers is therefore critical to understanding how signals evolve. In examining the potential for signals to be biologically relevant to receivers, I use the term *signal content* to refer, specifically and unambiguously, to: attributes of signalers that are associated with signal features in such a way that the signal can be a reliable indicator of the attributes. Signaler attributes may include intrinsic (e.g. sex, age, size), extrinsic (e.g. attention to a predator), or even behaviorally flexible

features (e.g. likelihood of attacking after producing signal). Signal features may include visual or acoustic characteristics (e.g. color, amplitude) and usage patterns. In examining the evolution of a signal, content, as defined, provides a model for how receivers' responses may relate to their own fitness priorities and thus be favored by selection, and neither requires nor suggests proximate conclusions about how signals operate.

Identifying the content of a signal is straightforward in principle: measure signaler attributes (e.g. size, sex, age) and signal features (e.g. duration), and look for relationships. Covariation between signal features and signaler attributes does not have to be perfect to be relevant; selection operates probabilistically and thus may favor consistent receiver responses even when the relationship is relatively small. A growing body of literature documents vocal signals across numerous taxa with content that includes signalers' **physical or physiological attributes** (e.g. body size in anurans, reviewed by Gerhardt & Huber 2002, and mammals, reviewed by Fitch & Hauser 2002; testosterone levels in some birds, Furlow et al. 1998, and giant pandas, Charlton et al. 2011), **social attributes** (e.g. dominance status in male baboons, Kitchen et al. 2003, and chickens, Leonard & Horn 1995; social group affiliation in bats, Masters et al. 1995), and the emergent attribute of **identity** (e.g. some birds, Robertson 1996, and numerous mammals, reviewed by Taylor & Reby 2010). In signals with high context specificity, content may also include **extrinsic attributes** (e.g. signaler's attention to predators, in squirrels, Sherman 1977, or food sources, in chickens, Evans & Evans 1999, or likelihood of moving, in some primates, Boinski 2000).

Signal content is an essential element of communication research, with applications for better understanding how signal systems are used and evolve and to explain observed

behavioral patterns. In addition to simply increasing our understanding of species and their signals, identifying content is critical to exploring functional hypothesis for signal usage and receiver responses (reviewed in Hauser 1996; Maynard Smith & Harper 2003). Furthermore, understanding relationships between receiver response and the signaler attributes to which signals relate can illuminate the biological importance of various social, physiological, and ecological factors for particular species – both currently and during their evolutionary history.

This Study

This chapter reports research on the signal content of vocalizations by adult male blue monkeys (*Cercopithecus mitis stuhlmanni*). More than three decades of research by Cords (2012) and colleagues has provided considerable insight into the social behavior of this species, yet their communication system is not well understood. Blue monkeys are group-living, arboreal, Old World monkeys that use a variety of distinct vocal signals. Their vocal behavior exhibits a high degree of sexual dimorphism, with the distinctive repertoire of adult males comprising six call types (see Chapter 2). Four of these – *boom*, *pyow*, *ka*, and *katrain* – are especially conspicuous "loud calls," with audible distances beyond the home range size of most social groups (Brown 1989), whereas the *ant* and *nasal scream* are somewhat quieter.

Adult males interact with conspecifics of different age, sex, and reproductive and competitive status, and in a range of affiliative and agonistic contexts. Furthermore, blue monkeys are vulnerable to several predators (e.g. snakes, eagles, leopards, dogs), with likely differences in what constitute adaptive anti-predator responses. The putative

importance of vocal signals in mediating these social and ecological circumstances, coupled with the acoustic distinctiveness and degree of within- and among-individual variation in structure and usage of the calls, suggests signal content is likely to be varied across the male repertoire. Only a few studies have examined blue monkey vocalizations (Marler 1973; Brown 1989; Brown et al. 1995), and only Butynski et al. (1992) examined potential content, demonstrating that acoustic features of *pyows* constitute reliable indicators of caller identity.

During 12 months of fieldwork in the Kakamega Forest, Kenya, I examined the vocal behavior of wild adult males, and used natural observations, playback experiments, and acoustic analysis of audio recordings to characterize content of all signals in the male vocal repertoire. I specifically tested the potential of call types to be reliable indicators of identity, social status, body size, and callers' attention to different extrinsic variables.

METHODS

Study Site and Subjects

Fieldwork took place from September 2010 – September 2011 in the Kakamega Forest in western Kenya. Details of the study site and species information are provided in Chapter 2 (pp 54-57), Cords (2012), and Lawes et al. (in press). Subjects were 32 adult males (Table 1), all known individuals from a population under observation since 1979. All subjects were identifiable by facial and body features.

Social status of subjects was assessed through daily monitoring of adult males and groups. For any period of observation, an adult male occupied one of three exclusive

social statuses: 1) *resident*: sole adult male observed consistently in a social group; 2) *non-resident*: either solitary or associating with other non-resident males, not in regular association with a particular heterosexual social group; or 3) *influx*: when multiple adult males were consistently observed with one social group (see Chapter 2, p. 56), all males in the group were considered influx males. During this study, I collected data from 32 male subjects holding resident (n=17), non-resident (n=16), and influx (n=10) status; some males held multiple statuses during the study period (Table 1). I also collected recordings and subsequent acoustic data for resident (n=17) and influx males (n=6).

Subjects were unequally sampled, with the vast majority of data coming from the resident males of five study groups. In these groups, all members are well habituated and individually identified, and information relating to age, parity, maternal relatedness, and social rank is known. During the study period, group size varied between 18-50 individuals, with considerable variation among groups in composition of adult (parous) females (range: 5-18), juveniles (nulliparous of either sex ≥ 2 years), and infants (< 2 years). Several other social groups, peripheral to the study groups and familiar to researchers at the site, were observed frequently; size and composition of these groups was unknown but appeared to fit the distribution of the study groups.

Data Collection

To examine relationships between features of vocal signals and attributes of male callers, I collected data relating to patterns of usage and acoustic structure of the different call types, and relating to callers' identity, social status, body size, and attention to particular external factors.

Call Production and Extrinsic Factors (Naturally Occurring)

Every day during the study period, 4-14 trained observers were distributed among different social groups and males (see Chapter 2, p. 58). Observers followed individual males from about 0730 h until 1730 h, typically suspending observation for ~1.5 hours around 1300 h. I sought to balance observations of the resident males of the five primary study groups for total hours, time of day, and number of days per month; observation times for non-resident males and residents of non-study groups were substantially lower and more varied (Table 1), but I still attempted to balance observations for time of day.

Data on male vocal behavior were recorded on an all occurrence basis (Altmann 1974). To distinguish levels of analysis, I used the nested categories of *Call*, a single, discrete vocal utterance (e.g. one *pyow*), *Bout*, a series of calls of one type (e.g. a bout of four *pyows*) with no other call types interspersed and ≤ 1 minute between calls, and *Episode*, any occurrence of vocal behavior by an individual male, and including all calls made by him with ≤ 1 minute between consecutive calls; episodes could comprise just one call (e.g. one *boom*), a bout (e.g. five *pyows*), or combinations (e.g. one *boom* followed by five *pyows* followed by two *ants*). Most episodes consisted of only one call type, given singly or in bouts, but combinations were not uncommon.

Whenever a male vocalized (i.e. any observed *episode*), observers recorded time, call type(s) and number, and caller's identity and location to the nearest 25m, using a gridded map of the study area (note: this applied to vocalizations by any male, though only cases in which caller was clearly observed and definitively identified were used in analyses). Observers recorded the context in which vocal behavior occurred narratively, noting the caller's activity just before and just after calling, activity of other monkeys in the vicinity,

and conspicuous social and ecological factors. Observers specifically noted the caller's attention (i.e. direction and intensity of orientation, level of vigilance behavior) and the presence or absence of predators, other males, other social groups, and conspicuous disturbances (e.g. tree falls, loud human activity). When appropriate, observations by several observers were combined for more complete assessment of context.

Identifying factors relevant to observed behavior is inherently difficult, and especially so in natural conditions where some things perceived by arboreal monkeys are beyond the earthbound and relatively myopic perspective of human observers. I was therefore extremely conservative, selecting for analysis only records in which the caller was well observed, context could be clearly determined, and the focus of the caller's attention was unambiguous. I excluded call records if multiple contextual variables were observed (e.g. predator *and* intruder male) or if the inferred provoking variable co-occurred with conspicuous social interactions (e.g. aggression between subject and group members).

Guided by extensive field observations and *post hoc* examination of records, I coded vocal episodes according to the presence of 15 external variables; secondary examination indicated some variables shared social or ecological characteristics such that combining variables was appropriate (e.g. snakes, dogs, and other ground predators were all "terrestrial threats"); accordingly, I reduced the original 15 variables to seven (Table 2).

External variables related to different social and ecological contexts, including abiotic disturbances (e.g. motorcycle), conspecific agonism (e.g. presence of other males), and predator encounters. At least four predators of blue monkeys occur at Kakamega: crowned eagles (*Stephanoaetus coronatus*), Gaboon vipers (*Bitis gabonica*), dogs (*Canis lupus familiaris*), and humans (Struhsaker & Leakey 1990; Cordeiro 1992; Foerster 2008;

Lawes et al. in press; pers. obs.). In addition to when predators were seen or heard, I assigned predator context, conservatively, in a few cases in which predator presence was not confirmed through direct observation but strongly inferred from predator-consistent behavior by other group members (climbing, diving, or mobbing, pervasive *chirp* or *growl* vocalizations, and hyper-scanning toward sky or ground) in the absence of other males or groups nearby, and radiating "alarm" calls by other species (e.g. colobus monkey, *Colobus guereza*, roars). Individually, these behaviors could relate to factors other than predators yet collectively are unlikely to relate to anything else. I likewise used extreme caution in labeling some records "Undisturbed" to describe contexts in which there was no other male or group observed nearby, no indication of predators, and no conspicuous disturbance, *and* the activity of both the caller and other monkeys before and after the episode was characterized by resting, feeding, and/or affiliative interactions. In contrast to other classifications, therefore, the category "Undisturbed," though often associated with a male's affiliative interactions with other monkeys, implies *absence* of external variables (i.e. receiver response is not linked to an entity extrinsic to the caller).

Call Production (Playback and Model Experiments)

To supplement natural observations and better isolate external variables associated with vocal behavior, I conducted field experiments with resident (n=7) and non-resident (n=7) males, simulating the presence of an "intruder" adult male blue monkey and different predator species through broadcast audio recordings or with a snake model. Similar experiments are known to reliably evoke context-appropriate responses in numerous birds (e.g. Illes et al. 2006) and mammals (e.g. Durant 2000), including several

primates (e.g. Waser 1977; Hauser & Wrangham 1990; Zuberbühler 2000; Ramakrishnan et al. 2005; da Cunha & Byrne 2006; Arnold et al. 2008). To avoid habituation, no subject received the same stimulus more than once and I did not conduct experiments on the same animal more than once in four days (Cuthill 1991).

To mimic another adult male nearby, I used playbacks of calls (*ant, boom, katrain, pyow*) recorded from different males throughout the study area. Each trial used recordings of males whose home range border was ≥ 500 m from that of the subject to reduce the likelihood that the subject would be familiar with the caller or his vocalizations. To simulate predator encounters, I used playbacks of vocalizations by crowned eagles (adults at nest, *quee-quee-quee-quee*), obtained from Macaulay Library (Cornell Labratory of Ornithology, NY), and domestic dogs (adult *bark* sequences), recorded outdoors in the United States. To avoid pseudoreplication, I used different recordings of predators and of calls by different males in each playback (Kroodsma 1989). Playbacks were broadcast from an iPod Classic (Apple, Inc.) through a Harman Kardon GO + PLAY Portable Loudspeaker (Harman International Industries, Stamford, CT). I pre-inspected all recordings for quality (e.g. lack of distortion and background noise) and broadcast calls at an amplitude of 93-104 db.

To examine response to snakes, I used a 0.92 m long fiberglass model of a Gaboon viper made from a mold of a real snake (Morgan Reptile Replicas, Liberty, NC), painted to realistic detail, and attached to a 100m spool of translucent fishing line (Fig 1). As control stimuli, I used recordings of non-alarm calls by local birds (e.g. black-and-white-casqued hornbills, *Bycanistes subcylindricus*, red-eyed doves, *Streptopelia semitorquata*,

and domestic roosters, *Gallus gallus domesticus*), and a plastic bag (i.e. an innocuous stimulus similar in size to a Gaboon viper).

Subjects were located and followed as part of normal daily observation, and observers carefully monitored subjects and associating monkeys for ≥ 60 min prior to experiments to verify there were no predator events, aggressive encounters, or vocalizations by any adult male (including subject) ≤ 30 minutes prior to trials. One observer surveyed the area to ensure no other groups or males were nearby, while another observer monitored the subject and I hung the speaker 2-5m up a tree, 30-50m from the subject. The speaker was positioned out of the subject's view, concealed in camouflage fabric, and pulled slowly into position so as not to draw attention. If the subject oriented toward the speaker or if other animals appeared to have detected it prior to playback, the trial was aborted.

Snake model experiments employed the same conditional requirements and observer roles. The model was concealed in a camouflaged sack and placed on the ground, out of sight of the subject and other monkeys, and covered with leaves. The experimenter uncoiled the fishing line along the ground, moving ~25m away from the model. The experimenter waited until the subject moved to a position affording an unobstructed view of the snake, then pulled the line, dragging the model from the sack and along the ground in a slow, rhythmic fashion simulating snakes' sidewinding locomotion (Fig 1).

Subjects' behavior was recorded continuously from one minute prior through 10 minutes after exposure to stimuli. Data recorded for each trial included type(s) and number of calls produced. I excluded from analysis trials in which subjects did not vocalize because the goal was to identify relationships between call types and particular external stimuli, rather than to ascertain the conditions under which males vocalize.

Audio Recordings and Acoustic Analysis

Digital audio recordings of male vocal behavior were made during systematic 3-hour focal samples, during playback and snake experiments, and opportunistically throughout the study. Details of recording equipment and methods are given in Chapter 2 (p. 59). I used Raven Pro 1.3 (Cornell Laboratory of Ornithology, Ithaca, New York) to perform discrete Fourier transform on digital recordings. With resulting spectrograms, power-time oscillograms, and power-frequency spectra, I measured 50 acoustic parameters relating to temporal and spectral elements of each call sample. Details of acoustic parameters and methods used to extract them are provided in Chapter 2 (pp. 60-62).

Body Size

The term "body size" is used in reference to several physical metrics, most commonly to describe overall skeletal length or body mass. In many species, both of these likely play important social roles, yet measuring animals in the wild is fraught with challenges; restraining animals can be difficult, dangerous, and expensive, and can adversely affect natural behavior and habituation. To minimize impact on subjects, I opted for a non-invasive technique.

Photogrammetry – using photographs to remotely measure objects – relies on the principle that photographs are, inherently, scaled representations. Spatial measurements from photographs, therefore, are possible if the scale can be accurately determined. This scale, in principle, is a function of the lens size and distance to the object, with the relationship between actual size of an object and its size on a photograph therefore

described by $S_A = D/F \times S_P$ where S_A is the object's actual size, D the distance from lens to object, F the lens focal length, and S_P the object's size on the photograph. Preliminary tests using an object of known size, however, resulted in consistently high differences between the calculated and actual size (i.e. error), suggesting the need for a *correction factor*, adjusting the above equation to $S_A = D/F \times S_P + C_i$, where C_i is a correction factor specific to the camera-lens configuration i.

To determine the correction factor for the camera-lens configuration I would use in the field (Nikon D300 with Nikkor 70-300mm telephoto lens), and to validate the aforementioned equation (the following methods are illustrated in Fig 2), I photographed a 30cm ruler from distances of 2-22m, at 2m increments, using several focal lengths at each distance. I loaded images on an Apple MacBook Pro computer, opened each in Adobe Photoshop CS, and used the "Measure" tool to obtain image size of the ruler.

For each image, I derived a calculated size using the above equation with a correction factor (C_i) set to 0.0, and then measured error as the difference between the calculated and actual size. I then regressed the error against $D \times F$ for all images (n=44), to identify the relationship between error and the interaction between distance and focal length of lens. This relationship was best described by a logarithmic trend line (Fig 2), from which I derived the appropriate correction factor (Table 3).

To validate the correction factor, I repeated the described process, photographing another premeasured object (mounted skeleton) 25 times from distances of 2-20m. I calculated size for each image using the previously derived correction factor, and again calculated differences between actual and calculated size. The average of all calculated

sizes was equal to actual size, and percentage of error (i.e. difference between calculated and actual size as a proportion of actual size) was extremely low (Table 3, Fig 2).

I applied this method to adult males in the field. I took ≥ 20 photographs per subject, using different focal lengths and from different distances. To measure distance from lens to subject, I used a Bosch DLR130K Digital Distance Measurer (Bosch Tool Corp., NA), which emits a red laser point and provides an almost instant reading accurate to ± 0.16 cm at 50m. Holding the distance meter at or near my forehead, I pointed the laser at the subject's torso and took measures until three consecutive measures were < 5 cm apart, and then recorded the average. I photographed subjects only if they were positioned parallel or nearly parallel to lens.

All images were uploaded and measured as described above. Measures used to calculate skeletal length include (Fig 3): **1) femur**, from midpoint of patella to the greater trochanter, **2) fibula**, from midpoint of patella to between the medial and lateral malleolus, **3) humerus**, from just below acromion to the olecranon process (note: the olecranon is the most lateral protuberance of elbow and is actually part of the ulna), **4) ulna**, from the olecranon process to the ulnar styloid process (bony protrusion above wrist, on side opposite thumb), and **5) vertebral column**, from midpoint of the cervical vertebrae to first caudal vertebra. Some landmarks related to these measures are difficult to estimate from photographs of animals covered in fur, and the resultant error likely accounts for some variation among calculated lengths.

For each subject, I calculated length of body parts for each image, using the equation detailed above, and used the average from all images as an estimated length for that

subject's skeletal measure (e.g. femur, fibula). For each subject, I then used the sum of these values as an estimate of his total skeletal length.

Statistical Analysis

In the following section, analyses of call types are grouped according to the caller attributes examined. All statistical analyses used R version 2.1 (R Development Core Team 2008), and tests were 2-tailed using $\alpha = 0.05$ unless otherwise specified.

Identity

To test whether call samples could be correctly assigned to different callers based on acoustic features, I used discriminant function analysis (DFA) and a cross validation using *leave-one-out* classification. DFA identifies linear combinations of predictor variables, or *discriminant functions*, that best distinguish among predetermined groups (e.g. individual callers) and then uses the discriminant functions to reclassify samples (Klecka 1980). The degree to which samples are "correctly" assigned can be used to assess how well different variables distinguish groups. Because of the relative rareness and subsequent low sample size for *ants*, *kas* and *nasal screams*, I examined only *booms*, *katrains*, and *pyows*. For analysis of each call type, because the number of recordings differed among males and unbalanced data sets can influence DFA adversely, I randomly selected equal numbers of recordings from different males (see Results, Table 4).

For DFA, I tested assumptions of homoscedasticity (Bartlett test of homogeneity of variances) and normality (Q-Q plot; i.e. data plotted against a theoretical normal distribution and visually assessed for departures from normality) for each acoustic

variable for each call type, and excluded variables accordingly (see Results, Table 4). For each call type, I used a forward stepwise linear discriminant procedure, with identity as the grouping variable and acoustic parameters as predictor variables, to construct linear discriminant functions (LDs). To cross-validate the resultant LDs, I used the *leave-one-out* classification procedure, using all call samples except one being classified, to assign samples to individuals. To test if calls were correctly assigned to callers more than expected by chance, I used a binomial test with the null probability derived from the number of males contributing to the data set (e.g. with five males, each call sample has a 0.2 chance of being correctly assigned). To identify acoustic variables that best distinguish among individuals for each call type, I examined the LDs and their canonical roots; in short, I assessed the discriminatory power of each LD from the proportion of variance among individuals it explained, and identified acoustic variables that contributed most to each LD by examining the LDs' canonical roots.

Social Status

For social status to qualify as content of a call type, it should be possible to distinguish a caller's status based on acoustic structure and/or usage of that signal. To characterize call usage, the unit of analysis was episodes per hour that included a particular call type (e.g. *pyow* rate was number of episodes containing at least one *pyow* per hour observed). I derived hourly rates for each subject for each call type based on the number of hours he was observed, and compared these across statuses.

It was apparent that males in non-resident status did *not* vocalize, except for *nasal screams*, a reticence in stark contrast to the frequent vocalizing of residents and most

influx males. The relatively lower observation times for non-residents (Table 1), however, reduces confidence that non-residents do not call at all (rather than less frequently), especially because asserting a zero probability of a non-resident's calling requires infinite observations. Instead, I used the observation times for non-residents to calculate a maximum rate of calling that was consistent with the observed lack of calling.

In a binomial experiment, the probability of an event (e.g. calling) occurring at least once in a series of trials is a function of the number of trials and the underlying probability of that event in each trial. This can be expressed as $P_{E\geq1} = 1-(1-P_E)^n$ in which $P_{E\geq1}$ is the probability of at least one occurrence in n trials when the probability of the event in each trial is P_E. Setting $P_{E\geq1}$ to 95%, therefore, sets a confidence interval and identifies P_E as the maximum probability of an event that was *not* observed in n trials.

I first generated a series of binomial distributions for possible call rates (i.e. P_E) from 1.0 – 0.0 calls per hour, extending n to 351 (i.e. total number of observation hours for non-residents). I treated one-hour periods of observation of non-resident males as independent trials (i.e. n), each with possible outcomes of *call* or *not call*. Because non-resident subjects were observed for different amounts of time, and I used two separate n: 1) total observation hours for all non-residents, pooled, and 2) more conservatively, total observation hours for each non-resident. I matched the number of observed hours to n on the binomial distributions and found the lowest corresponding call rate for which $P_{E\geq1}$ was ≥95%, and confirmed rates using a standard binomial test.

Males in influx status did vocalize, making it theoretically possible to compare call usage and acoustic structure between influx and resident males. The extremely small

sample sizes for observations and recordings of influx males, however, were inadequate for informative analyses; qualitative assessment is provided in Results.

Body Size

For each male, I estimated total skeletal length as described. For acoustic features, I used formant dispersion only. Formants (i.e. frequency peaks, seen as dark bands in spectrograms; see Chapter 2) reflect resonance frequencies of the signaler's vocal tract. These acoustic structures, and specifically the distance (i.e. dispersion) between them, vary predictably with body size in several mammal species (Fitch 1997; Riede & Fitch 1999; Reby & McComb 2003; Harris et al. 2006; Sanvito et al. 2007; Vannoni & McElligott 2008). This association relates to the fact that, in most mammals, skeletal length is strongly tied to length of the laryngeal tract (reviewed in Fitch & Hauser 2002), and the principles of sound production predict an inverse relationship between length of a chamber and formant dispersion (Fant 1960; Lieberman & Blumstein 1988; Fitch 1997).

To examine the relationship between skeletal length and formant dispersion, I used only *pyows*; acoustic structure of *booms* lacks formants (see Chapter 2, Fig 5), and recording sample sizes for *ants*, *kas*, *katrains*, and *nasal screams* were low. I selected the highest quality recordings of *pyows* by each male for whom I had skeletal length and then randomly selected 30 recording samples for each subject. For each sample, I extracted measures of formant dispersion (i.e. frequency difference between third and second frequency bands and between second and first bands) at 3-5 points (see Chapter 2, pp. 61-62). For each male, I used average formant dispersion value in analysis.

I regressed formant dispersion against skeletal length, and used a one-tailed Spearman rank correlation to test the relationship between the two variables; the small sample size and non-normally distributed data necessitated a non-parametric test, and the prediction that formant dispersion would correlate negatively with skeletal length (Fitch 1997) justified a one-tailed test.

External Variables

Naturally Occurring

From >10,000 records of naturally occurring vocal episodes, I created a subset (N=1344) by conservatively including only records for which caller was clearly observed, context was unambiguous, and only one conspicuous external variable was in evidence. To determine if some external variables could be considered signal content, I examined whether 1) call types occurred in association with particular variables more than expected by chance, and 2) call types were exclusively associated with particular variables. If call types were randomly associated with external variables, the expected frequency of a call type associated with a variable (e.g. number of *booms* occurring with *terrestrial threats*) is a function of the proportional occurrence of both the call type and variable (e.g. proportion of *booms* with *terrestrial threats* among all observed episodes). I calculated expected frequencies as $F_{Ecv} = (N_c \times N_v) \div N$ where F_{Ecv} is the expected frequency of call type **c** occurring with variable **v**, when N_c is the number of records with call type **c**, N_v the number of records containing variable **v**, and N the total number of records.

Whenever a call type occurred with a particular variable more than expected by chance, I tested the association using a binomial test. Specifically, I tested whether the

number of observations of the call type with the variable (e.g. number of *ants* associated with *terrestrial threats*), given all observations of the call type (e.g. number of *ants* with any variable), was significantly higher that expected by chance (i.e. F_{Ecv}). For repeated measures (i.e. cases in which a call type was positively associated with more than one variable), I used a Bonferroni-corrected alpha reflecting the number of repeated tests.

Experimental Stimuli

I examined data collected during experiments in a fashion similar to those from natural observation, though some modification was required. In playbacks, presence of another male was simulated by broadcasting calls; in most natural observation records, however, subjects called in response to another male that had *not* vocalized. Because hearing different call types might influence subjects' response to detection of another male, I separated *Other Male Nearby* trials by the call type that was played.

As with naturally occurring episodes, I calculated expected frequencies of each call type associated with each stimulus. Unlike natural observations, the restricted experimental contexts would likely reduce or exclude occurrence of some call types, making the proportional usage in trials less appropriate for deriving expected frequencies. I therefore calculated two sets of expected frequencies, on null hypotheses that 1) each of the five primary call types (*nasal scream* excluded) had an equal (20%) likelihood of occurring in a trial, or 2) a call type's likelihood in a trial was the same as in natural observations (i.e. proportional to natural usage).

As with data from natural observations, I examined differences between observed and expected frequencies of call types associated with each stimulus variable. For cases in

which a call type occurred with a particular variable more than expected by chance, I tested the association using a binomial test (as above).

Acoustic Variation within Call Type

In both natural observations and playbacks, *pyows* frequently occur in association with very different variables, and notably with both terrestrial threats (e.g. dogs) and other males (see Results). I tested whether *pyows* in these two contexts differed acoustically.

From digital recordings of *pyows* in which audio quality was good and context was clearly observed, I selected those associated with terrestrial threats and those associated with the presence of another male. Because variation in acoustic features among males was high, threatening to obscure possible inter-contextual variation, for each male I ensured the number of *pyow* samples from each of the two contexts matched.

To test whether *pyows* could be correctly assigned to a *terrestrial threat* or *other male* context based on acoustic features, I used discriminant function analysis (DFA) and a cross validation using *leave-one-out* classification. After testing assumptions of homoscedasticity (Bartlett Test of Homogeneity of Variances) and normality (Q-Q plot) as above, I used a forward stepwise linear discriminant procedure, with stimulus (i.e. terrestrial threat or male) as the grouping variable and acoustic parameters as predictor variables, to construct linear discriminant functions (LDs). To cross-validate the resultant LDs, I used the *leave-one-out* classification procedure, to assign samples to stimuli. To test if calls were correctly assigned more than expected by chance (with two contexts, 50% chance), I used a binomial test with the null probability 0.5.

RESULTS

Identity

Discriminant function analyses assigned 76%, 84%, and 71% of samples of *booms* (n=66), *katrains* (n=50), and *pyows* (n=135), respectively, to the correct caller; in each case, the proportion of correct classification was significantly higher than expected by chance (binomial test, 2-tailed $p < 0.001$), indicating the acoustic features were sufficient to differentiate among individuals. For *booms* and *katrains*, the first two linear discriminant functions (LD1-LD2) explained most of the variance, and for pyows the first three (Table 4; Fig. 4). The canonical roots of these LDs indicated that duration of the fundamental frequency (F0) and rise (i.e. time from start of call to loudest point) aided in distinguishing individuals in all three types, and especially so for *booms* and *pyows*; for *katrains*, the average inter-unit duration (i.e. time between end of one within-*katrain* unit and beginning of next) was most distinguishing among individuals.

Social Status

I collected data during natural observations and playbacks for 32 males in resident (n=17), non-resident (n=16), and influx (n=10) status (note: some individuals held multiple statuses during the study period). Observation times were highly unequal, with the vast majority of observation time with residents, and mostly with the residents of the main study groups (n=6; total: 4275 hrs; median: 861 hrs). Systematic follows of non-residents, residents of non-study groups, and influx males began later in the project, and observation times were typically sporadic.

Resident In playback and snake experiments, resident males (n=7) vocalized in 60% of non-control trials, and each resident vocalized in at least one trial (see *Experimental Stimuli*, below). All 17 residents vocalized during natural observations, and all call types were observed. The six residents with the highest observation times (median: 861 hours) typically vocalized every day (median: 5.7 episodes per day); the most common call types were *boom* (median: 0.44 per hour) and *pyow* (median: 0.38 per hour), with *katrains*, *kas*, and *ants* substantially less frequent (0.01-0.03 per hour; Table 5; Fig 5). On one occasion, a resident male *nasal screamed* during a fight with an unknown male.

Influx During this study, multi-male influxes occurred three times in two social groups. TWS group had 2-5 males consistently present during Sept-Oct 2010 and 3 males during Aug-Sept 2012, and GN group had 3 males during Aug-Sept 2012. Nine different males were observed in influx status (Table 1). Of these, three had been the prior sole residents and became influx males with the arrival of new males. Rates of calling for these three 'prior' males remained the same or increased slightly, and one *nasal screamed* during a fight with a new influx male.

Six subjects became influx males by entering groups. Because I prioritized the prior residents during influxes, observation time and audio recordings for new influx males were insufficient to assess differences with resident vocal behavior. All six new influx males produced *booms* and *pyows* at least once, four produced *ants*, two produced *kas* and *katrains*, and three produced *nasal screams* in fights with other males. New influx males appeared to call at lower rates than residents, though hourly rates were not

assessed. Non-quantitative aural and visual examination of influx males' recordings did not reveal conspicuous differences in call structure.

Non-resident The reported observation time for non-residents (total: 351 hrs; median: 21 hrs) is extremely conservative; some non-residents were observed periodically throughout the study period but, unfortunately, non-resident observations were not recorded systematically until the second half of fieldwork. During the 12 months of fieldwork, no male occupying non-resident status was ever observed to *ant, boom*, *ka*, *katrain*, or *pyow*. In playbacks and snake model experiments, no non-resident (n=7) vocalized in any trial (n=27). On three occasions, non-residents *nasal screamed* during fights with other males. To contextualize the observation that non-residents do not vocalize other than *nasal screams*, I calculated the maximum calling rate that could explain no episodes in the time non-residents were observed. When all non-resident observation hours were pooled, this rate was < 0.01 calls per hour; the more conservative estimate, using individual subjects' times, was ≤ 0.14 calls per hour (Table 5, Fig. 5).

Multiple statuses During this study, three subjects were observed in both non-resident and resident status, and six in both non-resident and influx (Table 1). In these cases, status predicted usage of calls: subjects that had been non-vocal as non-residents began vocalizing regularly upon entering or taking over groups; subjects that had exhibited typical vocal behavior as residents ceased vocalizing almost immediately after being deposed. Three subjects were observed in both influx and resident status (see *Influxes*, above), with no conspicuous differences in their usage calls.

Body Size

I used 11-16 photographs for each subject to calculate skeletal lengths (n=6; Table 6). The within subject variation in estimated length (Table 6, Fig 6), reflects measurement error likely related to subjects' posture and angle in images and difficulties in consistently measuring body parts covered in hair. Mean formant dispersion was negatively correlated with skeletal length (Table 6, Fig 6; one-tailed Spearman's rank correlation, ρ = -0.9856, n = 6, P < 0.002).

External Variables

Naturally Occurring

The subset of episodes in which a caller's attention to a particular external variable was unambiguous included 1344 records (Table 7). There were only seven observation records for *nasal screams*, each involving an intense aggressive encounter between males; though social groups were present during some but not all of these encounters, the caller's attention was unquestionably on the other male, and I labeled these "Other male (alone)," rather than split *nasal scream* records among two categories.

Among the 42 pairings (six call types, seven variables), there were 14 with values higher than expected by chance (Table 8, Fig. 7). Binomial tests showed significant positive associations for 1) *ants* with terrestrial threats, 2) *booms* with branch falls, 3) *booms* with undisturbed contexts, 4) *kas* with aerial threats, 5) *katrains* with aerial threats, 6) *nasal screams* with other males, 7) *pyows* with terrestrial threats, 8) *pyows* with other males, alone, and 9) *pyows* with other social groups, with or without males.

The *ant*, *ka*, *katrain*, and *nasal scream* were significantly associated with only one variable each. The positive associations of *kas* and *katrains* with tree falls, however, were close to significant (p=0.053 and 0.082, respectively). The *boom* and *pyow* were associated with three and four variables, respectively.

Experimental Stimuli

Resident (n=7) and non-resident (n=7) males were exposed to one of seven experimental or four control stimuli in 84 separate trials (Table 9). Residents vocalized in 60% of experimental trials and never during controls, and non-residents did not vocalize in any trial. Unexpectedly, no male vocalized to eagle playbacks, though response by females and juveniles in four of five groups appeared consistent with the presence of raptors (e.g. orient to speaker, move to cover, mob, sustained *chirps* and *growls*).

I used data only from trials in which males vocalized to examine association between call types and particular stimuli (Table 10; Fig. 8). Given a 20% chance of occurring in any trial, there were nine cases in which a call type occurred with a stimulus more than expected. When each of these was examined individually, binomial tests showed significant associations for 1) *booms* with other males who *boomed*, 2) *pyows* with other males who *anted*, and 3) *pyows* with other males who *pyowed*. The positive association between *pyows* and dogs was close to significant (p=0.033), as was that between *ants* and snakes (p=0.058).

When the null expectation was based on each call's usage in natural observations, the results were significant for 1) *ants* with dogs, 2) *ants* with snakes, 3) *kas* with other males

who *katrained*, and 4) *katrains* with other males who *katrained*. The positive association between *booms* and other males who *boomed* was close to significant (p=0.073).

Acoustic Variation within Call Type

I used discriminant function analysis (DFA) to test whether *pyows* associated with terrestrial threats differed acoustically from *pyows* associated with another male. I used a subset of 112 *pyow* samples from 11 males; each male's contribution to the *terrestrial threat* category was equal to his for *other male*, though number of samples per male varied (range: 6-14). The discriminant function correctly classified 58.9% of samples, not significantly better than the 50% expected by chance (binomial test, p=0.072).

DISCUSSION

There were clear relationships between signal features and signaler attributes across the vocal repertoire of adult male blue monkeys, indicating that vocal signals are reliable indicators of several intrinsic and extrinsic attributes. Here I discuss the findings and, for the purposes of future research, consider potential functional explanations relating to identified content and the possible mechanisms by which the reliability of signals is maintained.

Individual Identity

Results show that signal content for *booms*, *katrains*, and *pyows* includes caller's identity. That DFA assigned more than 75% of recording samples to the correct caller is

undoubtedly a conservative view of calls' distinctiveness, given that some loss associated with recording and measuring calls is likely. Analysis was performed on only half the repertoire, yet, the results and the structural similarity of *ants* and *kas* to *pyows* (see Chapter 2), identity is likely an element of content across all call types. In a closely related species, *C. nictitans*, however, one call type (*pyow*) was distinctive among individuals whereas another (*hack*) was not (Price et al. 2009); it is possible that some call types exhibit higher degrees of within-individual variation, thus swamping inter-individual differences.

The mechanism by which individual distinctiveness in mammalian vocal signals occurs and is maintained is likely quite simple, and undoubtedly relates to the enormous inter-individual variation inherent in their vocal anatomy (Fitch & Hauser 2002). In contrast to differences that constitute phenotypic polymorphisms (e.g. distinct color morphs), graded variation in the numerous folds, cartilages, muscles, and sinuses that make up the vocal anatomy cumulatively contributes to among-individual variation in vocal signals. In the male blue monkey calls, though some acoustic parameters were more useful than others, several features related to distinguishing callers, illustrating that identity as content is best considered an emergent property of variation in several features. Because the massive range of possible individual variation in mammalian vocal anatomy and production, signals given by different individuals, even signals selected to be highly stereotyped, are likely to differ, suggesting identity could be a near-ubiquitous element of content. In the context of the evolution of signals, therefore, it may be that identity is an unselected byproduct of inherent variation (i.e. selection has not favored homogenizing vocal production) rather than the result of selection having favored

advertising identity. Greater significance is thus conferred on selection favoring receivers using underlying variation to recognize individuals (Tibbetts & Dale 2007), and how doing so relates to responses.

Discriminating among individuals plays important roles in many social species, and is virtually essential to mother-infant relationships in most group-living altricial species. Evidence of individual recognition is widespread across diverse taxa, including mother-infant recognition in crèching birds (e.g. *Aptenodytes patagonicus*, Aubin & Jouventin 1998) and mammals (e.g. *Callorhinus ursinus*, Insley 2000), mate recognition (e.g. *Zosterops lateralis*, Robertson 1996), and recognition of kin (reviewed in Pfennig 2002) and non-kin individuals in social groups (e.g. *Loxodonta africana*, McComb et al. 2001). The "dear enemy" phenomenon illustrates the role of identity in mediating agonistic relationships among territory-holders (reviewed, primarily for birds, in Temeles 1994).

Recognizing individual identity is practically a hallmark of primates (Seyfarth & Cheney 2000), with responses specific to individuals documented across the major taxonomic divisions: apes (e.g. *Pan troglodytes*, Parr et al. 2000), strepsirrhines (e.g. *Lemur catta*, Palagi & Dapporto 2006), catarrhines (e.g. *Cercocebus albigena*, Waser 1975) and platyrrhines (e.g. *Callithrix jacchus*, Norcross et al. 1999). The complexity of most primate social systems, in which animals exhibit long-term, differentiated relationships with individuals who vary in a host of traits related to competition and reproduction, makes clear the numerous benefits associated with individual recognition (e.g. distinguishing kin and coalition members from others, using past experience to improve outcomes in repeated interactions).

Demonstrating that identity is an element of signal content in the calls of male blue monkeys is a first step in exploring potential functions of calls. Individual recognition based on vocal signals is likely to provide several benefits, primarily by allowing females and other males to monitor the presence of particular males from a considerable distance. Identity as content thus provides the potential to explain receiver responses to call types that are not associated with external factors (e.g. predators), as callers' location and identity alone may have relevance to receivers (e.g. based on social group membership). Identity as content also undoubtedly adds complexity to examining signal function, as receivers may modify their responses according to established relationships (e.g. Micheletta et al. 2012); caller attributes that are not signal content in and of themselves (e.g. social group membership) may therefore supplement (or replace) the relevance of other signal content.

Social Status

Patterns of use indicate that social status is an element of content in *booms* and *pyows*, but not in *nasal screams*; the relationship between status and usage of *ants*, *kas*, and *katrains* is less clear. Resident males vocalized regularly, typically producing *booms* and *pyows* several times daily, and *ants*, *kas*, and *katrains* at least a few times each month. Influx males also used the full repertoire of calls and, though rate and proportional usage may differ, call usage does not appear to greatly distinguish between resident and influx males. Observations indicate that non-residents do not *boom* or *pyow* and, if they do, it is far, far less than residents (even a generous estimate indicates non-residents call, at most, 2% – 37% as often as residents). Status likely also predicts use of *ants*, *kas*, and *katrains*

– non-residents never produced these call types – but the rareness of these calls and the low observation times for non-residents make this more difficult to conclude.

Social status is not signal content of *nasal screams*, at least as indicated by patterns of usage. Subjects classified as resident, non-resident, and influx males all used this call and with near absolute consistency of context: intense aggression between males, with the male that *nasal screamed* typically (but not always) the "loser."

Though signal content includes social status for at least some blue monkey calls, inferring how reliability is maintained is challenging. Researchers have identified predictable relationships between signal features and social dominance in various taxa (e.g. deer, Vannoni & McElligott, roosters, Furlow et al. 1998). In such studies, however, social dominance refers to an animal's relative position among regularly interacting conspecifics, with an individual's dominance rank calculated from outcomes of agonistic interactions (e.g. Rowell 1974; Hinde 1976; Zumpe & Michael 1986; Drews 1993; De Vries 1998). Dominance so defined, therefore, is not an attribute of an individual but rather of the agonistic asymmetry *between* individuals, and thus does not explain animals' responses to one another (i.e. an animal does not retreat from dominant animals *because* they are dominant). When signal features covary with dominance rank, it is likely that signal content includes particular attributes relevant to agonism (e.g. size, energetic condition, coalition partners) for which rank may be a cumulative proxy. In male baboons, for example, acoustic features of the *wahoo* call vary with dominance rank; it is, however, the relationship between these acoustic features and testosterone level, a predictor of stamina and aggressiveness and highly correlated with rank (Fischer

et al. 2002; Kitchen et al. 2003; Kitchen et al. 2005; Kitchen et al. 2009), that provides opportunity to explain receiver responses in biological rather than heuristic terms.

In regularly interacting animals (e.g. multi-male groups of baboons), it is possible to examine relationships among ordinal rank and continuous physiological (e.g. testosterone level) and acoustic features (e.g. duration, frequency). Adult male blue monkeys, however, rarely interact with one another. Furthermore, though males in the same status undoubtedly differ in several physical and physiological variables relating to individual RHP, call usage tracked changes from resident and non-resident status perfectly. This indicates that vocal behavior is categorically "on or off;" in other words, call usage by adult males, rather than exhibiting variation that might track continuous variation along a social status grade appears to be a two-class system (or possibly three-class, if influx males use calls at a lower rate). These observations bolster the conclusion that male vocal behavior (*nasal screams* excluded) is entirely conditional on being established with a social group, rather than relating to some other attribute for which status is a proxy; if calling were conditional on energetic condition, for example, we should expect some weaker resident males to cease calling before leaving a group, and some stronger non-residents to begin calling before moving into a group.

The reliability of male blue monkey vocalizations as indicators of status does not appear maintained by indexical properties (i.e. signal usage is not inherently tied to some physiological attribute relating to status), nor does it likely reflect Zahavi's (1975, 1977) handicap principle (i.e. call production is unlikely so energetically or physiologically costly that weaker males are *incapable* of calling). Though acoustic features of calls undoubtedly reflect variation in physical and physiological attributes relating to RHP, the

act of calling may be better described as a badge of status. Rohwer and Ewald (1981; expanding on ideas by Rohwer 1975, and Dawkins & Krebs 1978) characterized some animal signals as badges of status if honesty is maintained not by intrinsic costs of producing the signal but because doing so invites increased aggression, thereby favoring displays only by stronger individuals. Though this concept has been applied primarily to visual cues (e.g. color spots), the same principles could apply to vocal signals. In domestic roosters, for example, Leonard and Horn (1995), suggest that crowing, an energetically cheap signal (Horn et al. 1995), functions as a badge of status in light of evidence that dominant males crow at much higher rates than subordinate males, and subordinates that did crow were likely to be attacked afterward.

The ability of a male to maintain consistent presence in a group (the criterion used here to define male status) is undoubtedly associated with several attributes relating to competitive ability (e.g. age, size, condition). It is likely, however, that males occupying the same status would exhibit considerable variation in these attributes, and the rigidness with which calling appears associated with status, therefore, suggests that whether a male is inclined to call must relate to another attribute. It may simply be that calling reflects, directly or indirectly, a willingness to escalate aggression if challenged by another male. As such, calling by males in a social group – in addition to any other associated functions such as predator avoidance, group cohesion, etc. – could in and of itself function as an advertisement of occupancy, repelling less ambitious competitors.

Body Size

The inverse relationship between skeletal length and formant dispersion is sufficient to consider skeletal length content of *pyows*. Though I analyzed *pyows* only, the structural similarity of *ants* and *kas* to *pyows* (see Chapter 2) suggests size may be an element of signal content across more of the repertoire. The acoustic structure of *booms*, however, does not include formants indicating they are unlikely to include size as signal content.

Unlike signals for which reliability is maintained by being costly (handicap principle; Zahavi 1975, 1977), the *pyow* as an indicator of size exemplifies an indexical cue; the relationship between formant dispersion and body size is tied to intrinsic properties of mammalian skeletal morphology and sound production (Fitch & Hauser 2002). Selection cannot favor violation of the laws of physics and evidence of a consistent relationship between body size and vocal signals across taxa (reviewed in Fitch & Hauser 2002; Reby & McComb 2003; Charlton et al. 2009) suggests that strategies for concealing smallness (e.g. not vocalizing) are likely to evolve more easily than mechanisms for falsely advertising largeness. Assuming that "sounding larger" benefits signalers and bears little cost, we might expect mutants to invade with signals whose acoustic structure does not accurately reflect size. In blue monkeys, this could be achieved by facultatively lowering the larynx when calling (e.g. red deer, Reby & McComb 2003) or inflating the supralaryngeal air sac (Fitch & Hauser 2002; Hewitt et al. 2002) to achieve lower formant dispersion; as Harris et al. (2006) point out for guereza (*Colobus guereza*) roars, however, such strategies may exaggerate 'advertised' body size in terms of expected relationships between size and acoustic structure, but *within* a species are likely fixed traits and thus still reliable indicators of relative size.

In many species, when individuals compete for resources (e.g. male-male competition for access to reproductive females), the result of contests is typically based on contestants' relative resource-holding potential (RHP), an emergent property of attributes such as body size, energetic condition, fighting ability, age, and experience (Parker 1974; reviewed in Arnott & Elwood 2009). Direct aggression, however, is likely to cost even victorious contestants in terms of energy and injury, and selection should thus favor signals that function to preemptively resolve contests (reviewed in reviewed in Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003). As discussed in the Introduction, for such signals to function (e.g. for selection to favor receivers retreating), they should be reliably associated with some attribute relating to RHP. Because larger contestants tend be the winners in direct aggressive encounters (reviewed in Arnott & Elwood 2009), it stands to reason that signals that function in contest competition would include body size as content.

The biological importance of body size, and thus its relevance to communicative signals, may also relate to mate choice, as females in many taxa preferentially mate with larger bodied males (reviewed in Andersson 1994). Though unequivocal evidence that advertising body size in vocal signals directly influences mate choice is extremely difficult to obtain (Snowdon 2004), a compelling body of indirect evidence continues to accumulate. For example, red deer females preferentially approach vocalizations manipulated to reflect larger body size (Charlton et al. 2007), and the same is seen in several anuran species (reviewed in Gerhardt & Huber 2002). Phonotaxis, however, though inferentially useful, does not confirm mate choice and considerable research is still required to understand the relationship between vocal signals and mate choice,

especially in primates. In primates, where reproductive decisions are likely based on numerous different factors (e.g. size, social status, novelty, energetic condition, likelihood of parental care) and repeated interactions play an important role (reviewed in Dixson 1998; Setchell & Kappeler 2003), reproductive behavior "in response to" vocal signals may not always be immediate.

In blue monkeys, adult males compete with one another for access to females, with typically one sole resident striving to maintain his harem from other males who seek to take his place directly (i.e. harem takeover) or indirectly (e.g. sneak copulation). As with other species exhibiting one male social systems, it is likely that a male's body size relates to success in aggressive encounters and thus lifetime reproductive success (reviewed in Clutton-Brock 1989). Body size as signal content, therefore, might provide inference for how signals function if male receivers avoid calls of larger males, as seen in several other species (e.g. anurans, Gerhardt & Huber 2002; deer, Reby et al. 2005). Ghazanfar et al. (2007) demonstrated that captive rhesus monkeys can match images of larger animals to recordings of vocalizations with lower formant dispersion; in the wild, however, it remains to be seen whether animals attend specifically to this acoustic variation. It is also worth emphasizing that the content in *pyows* is skeletal length and, though inherently correlated, is not a perfect predictor of body mass. Skeletal length is unlikely to change in adulthood, whereas muscle mass, likely a more important predictor of an animal's RHP, may change in relation to season, age, and individual fortunes.

External Variables

A growing number of studies across taxa demonstrate that some signals can be associated with specific external objects or events (reviewed in Furrer & Manser 2009). Researchers have emphasized the importance of such stimulus specificity to the evolution of alarm calls (reviewed in Cheney & Seyfarth 1990) and, perhaps to a lesser extent, to calls associated with rallying conspecifics (e.g. food calls, reviewed in Clay et al. 2012). Vocalizations that are acoustically distinct and produced primarily with a particular external stimulus provide the opportunity for selection to favor a consistent response by receivers (e.g. in vervet monkeys, the "eagle call" is predictably given in response to eagles, and upon hearing the call, receivers consistently seek cover; Seyfarth et al. 1980).

In examining whether calls have the potential to be "functionally referential" (*sensu* Marler et al. 1992), the first task is to identify whether external variables are included in signal content. Importantly, for an external variable to be considered content the association between signal and variable should be more or less exclusive; if calls are associated with multiple, dissimilar stimuli, relating receiver response to any one of them is likely unwarranted.

Four call types – *ants*, *kas*, *katrains*, and *nasal screams* – were reliable indicators of particular external variables whereas *booms* and *pyows* were not. This distribution of content likely reflects selection favoring high specificity of content to achieve some functions (e.g. predator avoidance) that is not required for others (e.g. advertisement of occupancy).

Ants, *Kas*, and *Katrains*

Three of the male calls were unambiguously associated with specific types of external threat. The consistency and specificity with which *ants*, *kas*, and *katrains* were used in association with predators suggest they likely function by reducing predation on callers, their kin, and/or mates, by stimulating predator-avoidance behavior in receivers or causing predators to redirect or terminate their attack (Sherman 1977; Hasson 1991). Though sharing a functional class, the mechanisms by which these calls achieve reliability and function likely differ. The occurrence of acoustically distinct alarm calls in the same repertoire, with *ants* used primarily with terrestrial threats and *kas* and *katrains* with aerial threats, is consistent with the hypothesis that distinct signals evolve when species face multiple predators whose differences in hunting behavior demand distinctly different avoidance responses (Marler 1977; Macedonia & Evans 1993).

Ants were used with extremely high consistency with terrestrial threats, and perhaps slightly more with snakes than other disturbances. In natural observations and stimulus trials, *ants* were commonly associated with observed snakes and in many cases that were *consistent with terrestrial predator*, behavior of caller and other monkeys suggested snake events. That *ants* were also significantly associated with dogs supports the view of a generalized terrestrial disturbance call and, though the call's rareness gives greater statistical import to what might be anomalous observations, *ants* also occurred in response to baboons, civets, and motorcycles. Though not systematically evaluated, observations suggest *ants* are more likely when callers actually see a ground predator whereas *pyows* occur when callers perceive a predator acoustically (e.g. dog barks, alarm *chirps* by other monkeys) and/or from a distance; the acoustic similarities between *pyows*

and *ants* and the tendency for extended *pyow* bouts to grade into *ants* (see Chapter 2) may therefore reflect that, on a mechanistic level, caller arousal dictates call structure (Morton 1977; Owren & Rendall 2001) and is sufficiently specific to terrestrial threats to allow *ants* to be functionally referential (Seyfarth & Cheney 2003; Furrer & Manser 2009).

Kas and *katrains* were used with extremely high consistency with aerial threats. Observations suggest that males may discriminate among species, often not calling in response to black kites (*Milvus migrans*) or other species unlikely to prey on monkeys, yet calling predictably to eagles and other large raptors. However, the calls' use in association with airplanes is consistent with a generalized aerial alarm function. As with most natural phenomena, the association between *kas* and *katrains* and aerial threats was not perfect; calls were also given in response to dogs, loud trucks, and trees falling nearby, with the associations between each call and the latter nearly significant. The overall relationship with aerial threats, however, was strong (~80% of *kas* and *katrains* were associated with aerial threats; Table 4) and likely sufficient for selection to favor receivers responding with behavior for avoiding aerial predators.

The benefits of two distinct alarm calls in blue monkeys are clear. Relative to terrestrially bound species, arboreal animals may have more options for responding to threats, and the choice should depend largely on the position and hunting strategy of the predator (e.g. raptor: climb down and under cover; snake: climb up and mob). Though signals with *any* predator as content could relate to function if they stimulate increased vigilance in receivers, the acoustic distinctiveness and specificity with which blue monkey alarm calls are used suggest they enable predator specific responses by receivers.

Receiver response to these calls will be examined in a subsequent chapter, but the signal content alone provides some inferences for their possible function. Though an adult crowned hawk eagle weighs less than 5kg (Kemp 1994), they frequently prey on animals larger than adult male blue monkeys (6-7 kg; Delson et al. 2000; Colyn 1994), including other primates weighing three times as much (Mitani et al. 2001). The consistent association of *katrains* and *kas* with raptors therefore suggests these calls function by prompting receivers to seek cover (*conspecific warning hypothesis*, Maynard Smith 1965), and possibly by discouraging the raptor itself (*perception advertisement hypothesis,* Sherman 1977; Hasson 1991; Flasskamp 1994); the absence (or at least relative rareness) of these calls by non-resident males suggests the former is a primary function. Snakes are unlikely to prey on adult males, suggesting *ants* may function by drawing receivers' attention to either the caller or the ground, and possibly encouraging mobbing. Despite the enormous differences between dogs and snakes, the use of *ants* with both predators suggests that, for arboreal monkeys they are categorically the same in terms of what constitute appropriate predator avoidance strategies (e.g. climb up, keep predator in view); this is in contrast with a terrestrial species like suricates that have evolved distinct calls to snakes, jackals, and raptors (Manser 2001).

Nasal screams were used consistently during intense aggression with other males. This unambiguousness of context clearly suggests a function in male-male agonism and, given the appearance that losers are the more likely to scream, potentially as a submissive gesture. As such, signal content most relevant to the call's putative function likely relates to a caller's probability of retreat, making the presence of another male a seemingly

minor and likely unselected content element. Conspicuous vocal signals, however, are perceived by several different animals at a time, and responses by many different receivers may therefore relate to selection for, or limitations on, a signal; though the notion of "intended receivers" and singular functions based on one response type provides a convenient framework for examining primary selection mechanisms, it is important to consider the multidimensional space in which signals evolve.

In some primates, screams are produced in aggressive contexts, and appear to function by recruiting others to support the screamer (e.g. rhesus monkeys, Gouzoules et al. 1984; chimpanzees, Goodall 1968; Slocombe & Zuberbühler 2007); observations of adult female and juvenile blue monkey screams suggest they may function similarly (pers obs; pers. comm. M. Cords). For adult male blue monkeys, however, such a function seems unlikely; males do not form coalitions and females, being nearly 40% smaller (males ~6.2 kg; females ~4.0 kg; Delson et al. 2000; Colyn 1994), are unlikely to fare well intervening in a male fight. Indicating another male's presence may, however, provide minor benefit if doing so solicits females to draw closer to contestants, potentially changing the attention of an aggressor.

Booms and *pyows* were each used in a variety of contexts and in association with several external variables, and therefore neither calls' content includes external variables. Results of natural observations and playbacks, for example, indicate the strong positive association between *pyows* and dogs, consistent, perhaps, with *pyows'* association with leopards reported in other populations of this species (Papworth et al. 2008). *Pyows*, however, were also associated with agonism (e.g. presence of another male), and were

also frequently given when no disturbance was observed (consistent with "spontaneous" vocal behavior). This lack of exclusivity precludes the *pyow's* being considered referential of any particular external variable, and suggests the call derives function from other content. Inclusion of identity and status alone may allow *pyows* to function in a variety of social contexts simply by drawing attention to the caller's presence (e.g. maintaining group cohesion, repelling intruder males) and its frequent use and audible distance of >1000m (Brown 1989) further supports a view of the *pyow* as an advertisement of occupancy.

Booms were used in some contexts grouped broadly as ecological disturbances – during minor earthquakes, after thunder, and, with curiously high consistency, after tree branch falls – yet the vast majority of *booms* were observed during peaceful social contexts. The function of this call (to be explored in the following chapter) strongly appears related to facilitating affiliative interactions with females, perhaps similar to grunts by male baboons (Palombit et al. 1999) and thus may derive benefit as a reliable signal of the caller's behavioral intention (i.e. *benign intent*; Silk 2002). The *boom*, however, is estimated to be audible to other monkeys nearly 1000m away (Brown 1989), suggesting that its function in close encounters with group mates may be only one source of benefit. The fact that males tended to *boom* in response to *booms* by other males (in playback trials, but also in some natural observations) is both intriguing and puzzling.

Conclusion

Results demonstrate that vocal signals by male blue monkeys are rich in content, with some simultaneously including identity, status, size, and external variables, in addition to

the presumed content of species, sex, and other attributes yet to be explored. By examining the entire male repertoire, this study also illustrates how content elements are distributed unequally across signals, and provides a starting point for examining how selection may favor divergence of signals and the expansion of repertoires.

Identifying signal content has numerous applications to examining vocal behavior of this species, including assessing signal function, interpreting receiver responses (from ultimate and proximate perspectives), and in comparative studies with other species for insight to how signals diverged over evolutionary time. It is important to acknowledge, however, that the content identified in this study does not constitute an exhaustive list for male blue monkey vocalizations, and that identifying signal content does not confirm its relevance to or reception by receivers; future study is necessary to fully understand the relationship between specific elements of content and receiver responses.

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Table 1. Total observation hours and number of vocal episodes observed and digitally recorded for each adult male, with social status and group affiliation at time of observations; some subjects occupied multiple statuses during the study period. The first 6 subjects received the highest observation hours.

SUBJECT	SOCIAL STATUS	SOCIAL GROUP	HOURS OBSERVED	VOCAL EPISODES OBSERVED	VOCAL EPISODES RECORDED
PER	Resident	GSC	867.50	912	68
SAW	Resident	GSA	873.10	1231	105
MARV	Influx	TWS	381.90	389	12
	Resident	TWS	633.20	846	81
PH	Resident	GN	853.80	1109	113
	Influx	GN	137.60	139	10
QUAC	Non-resident	n/a	17.16	0	0
	Resident	TWN	939.60	1011	117
TIP	Resident	TWS	107.40	111	7
	Influx	TWS	217.60	248	21
	Non-resident	n/a	39.72	0	0
ABE	Non-resident	n/a	31.32	0	0
DIET	Non-resident	n/a	17.64	0	0
DURH	Non-resident	n/a	7.80	0	0
ELV	Non-resident	n/a	15.48	0	0
HOS	Non-resident	n/a	29.16	0	0
ROC	Non-resident	n/a	23.40	0	0
SCUL	Non-resident	n/a	20.64	0	0
SHRED	Non-resident	n/a	21.36	0	0
VANI	Non-resident	n/a	32.16	0	0
AXE	Resident	NE	*	26	2
FEZ	Resident	GSB	*	31	0
IDI	Resident	F	19.7	27	7
KENT	Resident	F	*	19	3
NE-MALE	Resident	NE	*	6	2
NW-MALE	Resident	NW	*	11	3
POP	Resident	TE	*	79	17
TIGE	Resident	ExF	*	12	0
XER	Resident	P	*	2	0
ZOMB	Resident	GSB	*	78	0
RAF	Influx	GN	*	7	5
WART	Influx	TWS	50.5	21	1
CHAM	Influx	TWS	15.00	3	0
	Non-resident	n/a	13.56	0	0
FLIP	Non-resident	n/a	16.06	0	0
	Resident	F	*	78	12
KL	Non-resident	n/a	37.32	0	0
	Influx	TWS	70.20	20	4
MWIZ	Non-resident	n/a	20.52	0	0
	Influx	TWS	33.50	10	2
SQUIR	Non-resident	n/a	7.32	0	0
	Influx	TWS	*	10	0
	Influx	GN	*	54	18

* Observation times for some males were recorded irregularly. Records from starred males were not used to calculate rates of calling.

Table 2. External variables associated with call episodes. Each call record was scored according to the presence of and caller's attention to one of 15 external variables. For secondary analysis, some variables were merged into single categories based on social or ecological similarities and behavioral response.

EXTERNAL VARIABLE	DESCRIPTION	MERGED VARIABLE
Tree fall	Entire or large part of tree falling nearby w/ loud crash.	n/a
Branch fall	Branch falling nearby, quieter than tree fall.	n/a
Dog	Seen or heard.	Terrestrial Threat
Snake	Seen (species not distinguished).	
Human	Non-familiar (i.e. not researcher; e.g. wood gatherer, cowherd, hunter). Note: dogs often accompany people, though were not *observed* in 'Human' cases. It is likely that for at least some 'Human' records the evoking stimulus was actually a dog.	
Predator consistent (non-specific terrestrial)	No other group or adult male seen nearby. Prolonged *chirps* throughout caller's group, monkeys look down and climb up. Radiating vocalizations from other species (e.g. colobus *roar*, redtail monkey *chirp, ant*).	
Machine (terrestrial)	Loud vehicle (truck, motorcycle, car, tractor).	
Raptor	Seen (species not distinguished).	Aerial Threat
Predator consistent (non-specific aerial)	No other group or adult male seen nearby. Prolonged *chirps* and *growls* throughout group, monkeys look up and dive down. Radiating vocalizations from other species throughout area (colobus *roar*, redtail monkey *chirp*, hornbill scream).	
Machine (aerial)	Airplane, helicopter.	
Other male (alone)	Adult male seen nearby, no other social group seen. Behavior of subject and 'intruder' ranged from intense scanning and/or moving, to overt aggression (chase, lunge, grab).	n/a
Other male (with social group)	Adult male nearby, with his group. Interactions between caller and male as above. Interactions between groups typically (but not always) aggressive.	Other Social Group (w/ or w/out male)
Other social group (no male observed)	Social group other than caller's nearby, with interactions between the social groups typically (though not always) aggressive. Caller's attention was to other group, with no other male seen; it is likely, however, that in some cases the other group male was present though not observed.	
Approach (non-aggressive)	No other social group, male, or predator seen, and no other conspicuous social or ecological disturbance. Just before calling, caller approached or was approached by female or juveniles (often producing *long grunts*). No aggression observed before or after calling, with caller typically resting, feeding, or grooming with or near approached animals.	Undisturbed
Resting ("spontaneous")	No other social group, male, or predator seen, and no conspicuous social or ecological disturbance. Activity of caller before and after calling was resting, feeding, or grooming, with no conspicuous vigilance or self-directed behavior. General activity of monkeys nearby before and after call was same.	

Table 3. Results of tests to derive correction factor for calculating size from photographs. Validation tests of the derived correction factor (using skeleton) resulted in a mean estimated size equal to actual size. Error (difference between actual and estimated size) is presented as percentage of actual size.

Camera-Lens Configuration	Correction Factor	Mean Error: Actual – Estimated size (n=25)	ERROR (absolute values)				
			Min	1st Quartile	Median	3rd Quartile	Max
Nikon D300 w/ 70-300mm lens	1.074ln(DxF) - 10.597	0.00 cm	0.02%	0.50%	1.03%	1.78%	6.72%

Table 4. Results of DFA. Proportion of samples assigned correctly to individual callers was larger than expected by chance. For each call type, proportion of variance explained by the first two linear discriminant functions is given, along with the acoustic variables with highest coefficients (i.e. variables that best describe variance among males).

CALL TYPE	SAMPLES (# males)	ACOUSTIC VARIABLES (Chap 2, Table 2)	CORRECTLY ASSIGNED		VARIANCE EXPLAINED	
			Expected by chance	Actual (range)	LD1 Coefficient Variables	LD2 Coefficient Variables
BOOM	66 (6)	1, 4, 6-11, 14, 15	0.167	0.758 (0.46-0.91)	0.84 Dur_tot: 96% Rise_rel_tot: 4%	0.10 Dur_tot: 99%
KATRAIN	50 (5)	1, 6, 8, 9, 11-15, 49, 50	0.200	0.840 (0.6-1.00)	0.84 Inter-unit_dur: 60% Rise_rel_tot: 33%	0.12 Intr-unit_dur: 80% Dur_tot: 17%
PYOW	135 (9)	1, 6-12, 15, 17-19, 23, 24, 46-48	0.111	0.71 (0.53-1.00)	0.42 Dur_tot: 99%	0.24 Dur_tot: 74% Rise_abs.F0: 24%

Table 5. Average rates of usage of each call type derived from (left) the six residents with the highest observation hours, compared to (right) the hypothetical maximum rate that could explain, with 95% confidence, no calls observed in non-residents.

	CALL TYPE	HOURLY RATE Mean (SD)		OBSERVATION HOURS USED TO DERIVE RATE	MAXIMUM HOURLY RATE Mean (range)
Resident males (n=6)	ANT	0.01 (0.01)	Non-resident males (n=16)	350.6 All non-residents, hours pooled	0.009 (n/a)
	BOOM	0.44 (0.08)			
	KA	0.02 (0.01)			
	KATRAIN	0.03 (0.02)		7.3 – 39.7 All non-residents, hours for each male	0.14 (0.08 – 0.34)
	PYOW	0.38 (0.07)			
	ANY CALL	0.81 (0.06)			

Table 6. Skeletal length and formant dispersion for the six males used in analysis. Within-subject variation in skeletal length reflects measurement error. Spearman's rank correlation (one-tailed) indicated a significant negative correlation between the variables.

SUBJECT	SKELETAL LENGTH (cm) Mean (IQR)	FORMANT DISPERSION (Hz) Mean (IQR)	ρ =	P =
TIP	114 (109-119)	462 (452-469)	-0.9856	0.00016
SAWA	115 (109-119)	371 (364-375)		
QUACK	116 (112-119)	369 (358-378)		
PERCY	120 (115-123)	349 (346-353)		
MARVIN	120 (115-123)	317 (312-330)		
PH	122 (116-125)	291 (281-310)		

Table 7. Summary of records of naturally occurring vocal episodes included in analysis. The number of observations of each call type's occurrence with each variable is given, using the merged variable categories described in Table 2.

	Tree Fall	Branch Fall	Terrestr Threat	Aerial Threat	Undisturbed	Other Male (alone)	Other Group (w/ or w/out male)	TOTAL episodes w/ call
ANT	7	0	36	5	0	6	5	**59**
BOOM	8	57	28	4	131	38	131	**397**
KA	4	0	0	19	0	0	1	**24**
KATRAIN	14	0	8	118	0	5	3	**148**
NASAL SCREAM	0	0	0	0	0	7	0	**7**
PYOW	40	11	151	72	33	119	283	**709**
TOTAL episodes w/ variable	**73**	**68**	**223**	**218**	**164**	**175**	**423**	**1344**

Table 8. Naturally occurring cases in which a call type was associated with a particular variable more than expected by chance. Two-tailed binomial tests revealed nine that were significant (shaded). Calls associated with >1 variable are not exclusive.

CALL TYPE (corrected alpha)	EXTERNAL VARIABLE	BINOMIAL TEST P value	Number of significant associations
ANT (0.025)	Tree Fall	0.141	1
	Terrestrial Threat	< 0.0001	
BOOM (0.0167)	Branch Fall	< 0.0001	2
	Undisturbed	< 0.0001	
	Other Social Group (w/ or w/out male)	0.386	
KA (0.025)	Tree Fall	0.053	1
	Aerial Threat	< 0.0001	
KATRAIN (0.025)	Tree Fall	0.082	1
	Aerial Threat	< 0.0001	
NASAL SCREAM	Other Male (alone)	0.0047	1
PYOW (0.0125)	Tree Fall	0.7519	3
	Terrestrial Threat	< 0.0001	
	Other Male (alone)	0.0036	
	Other Social Group (w/ or w/out male)	0.0001	

Table 9. Summary of experimental trials. The number of trials involving residents and non-residents is given for each of the 11 stimuli, along with the number of trials in which subjects responded with each call type or no vocalization (note: non-residents never vocalized). Some subjects produced more than one call type during some trials, thus the number of responses is higher than the number of trials.

CLASS	STIMULUS	TRIALS		VOCAL RESPONSE (number of trials that included each call type)					
		Non-res males (n=7)	Resident males (n=7)	PYOW	BOOM	ANT	KA	KATRAIN	NONE
PREDATOR	Eagle	4	5	0	0	0	0	0	9
	Dog	5	7	4	0	3	0	0	7
	Snake	5	6	1	1	3	0	0	7
MALE NEARBY	*Ant*	0	4	3	0	0	0	0	1
	Boom	3	6	1	4	0	0	0	5
	Katrain	5	7	3	1	0	2	3	7
	Pyow	5	7	4	1	0	0	0	8
TOTAL (non-control)		**27**	**42**	**16**	**7**	**6**	**2**	**3**	**44**
CONTROL	Hornbill	1	2	0	0	0	0	0	3
	Dove	2	2	0	0	0	0	0	4
	Bag	2	2	0	0	0	0	0	4
	Rooster	2	2	0	0	0	0	0	4
TOTAL (control)		**7**	**8**	**0**	**0**	**0**	**0**	**0**	**15**

Table 10. In stimulus trials, cases in which a call type was associated with a stimulus more than expected by chance. Two-tailed binomial tests revealed three that were significant when expected occurrence was 20% and four when based on frequency in natural usage.

CALL TYPE (corrected alpha)	STIMULUS	P value (Expected chance: 20%)	P value (Expected chance: natural usage)
ANT (0.025)	Dog	0.148	< 0.001
	Snake	0.058	< 0.001
BOOM	Male nearby (who *boomed*)	0.007	0.073
KA	Male nearby (who *katrained*)	1.000	0.007
KATRAIN	Male nearby (who *katrained*)	0.396	0.022
PYOW (0.0125)	Dog	0.033	1.000
	Male nearby (who *anted*)	0.008	0.251
	Male nearby (who *katrained*	0.396	0.3266
	Male nearby (who *pyowed*)	0.007	0.377

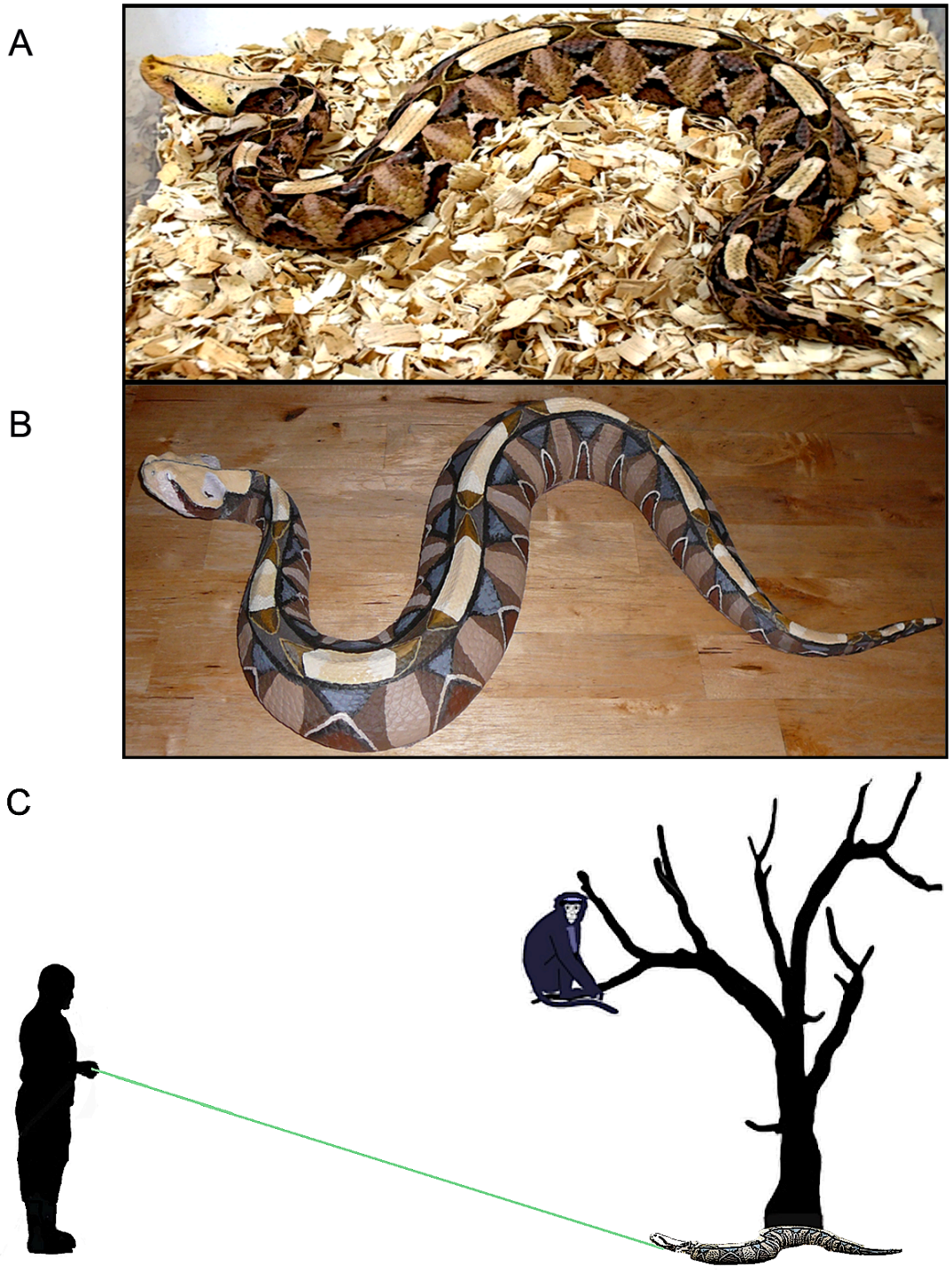

Figure 1. An actual Gaboon viper (A), compared to the painted fiberglass model (B) used in simulations. During exposure trials (C), the experimenter stood ~25m away from the subject and pulled the model along the ground using translucent fishing line.

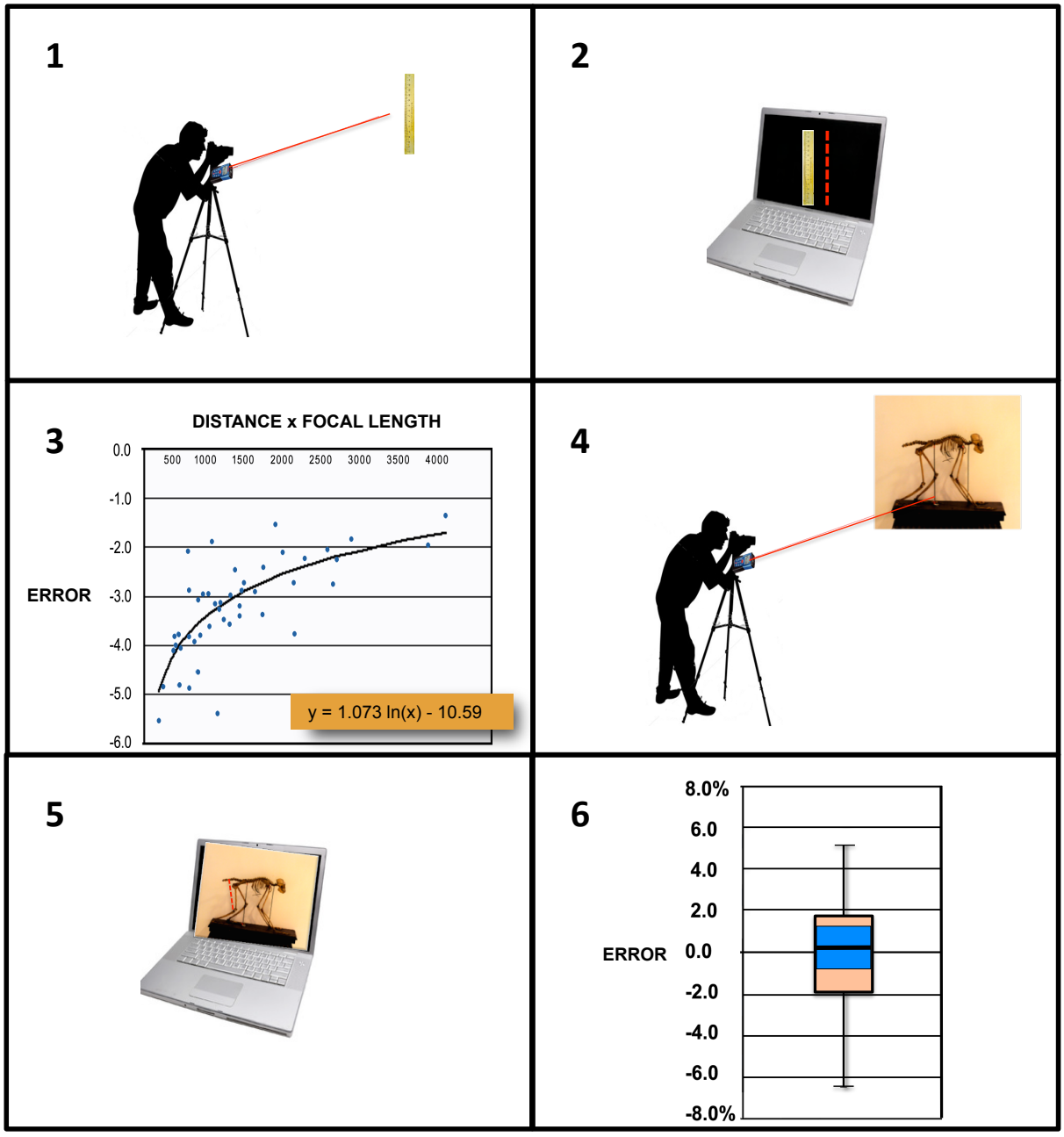

Figure 2. Method for deriving and validating correction factor to measure body size. **1)** photograph ruler at various distances and focal lengths; **2)** measure in Photoshop; **3)** regress error (actual - estimated size) against distance x focal length for each image; equation describing this relationship is correction factor; **4)** photograph skeleton from various distances; **5)** calculate femur length using correction factor; **6)** in validation test, median error was 0.16% above actual size; 50% of error was < 1.1% (blue box), with 80% < 2% (pink box); whiskers show remaining 20% of error.

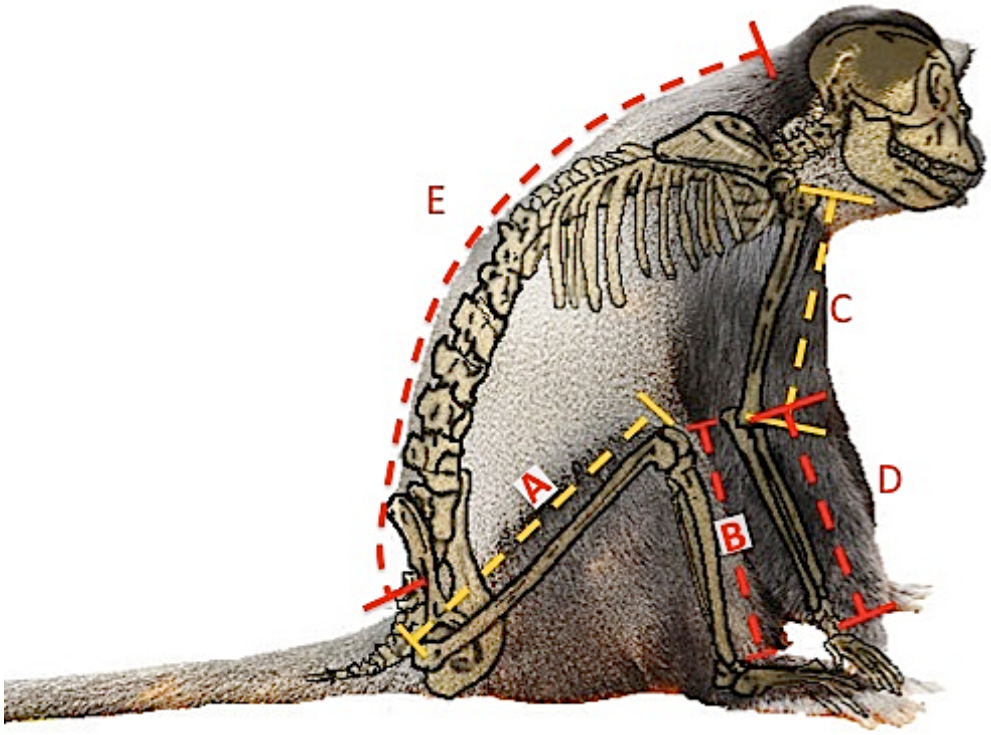

Figure 3. Skeletal measures taken from photographs of subjects, as described in methods. A) femur, B) fibula, C) humerus, D) ulna, E) vertebral column.

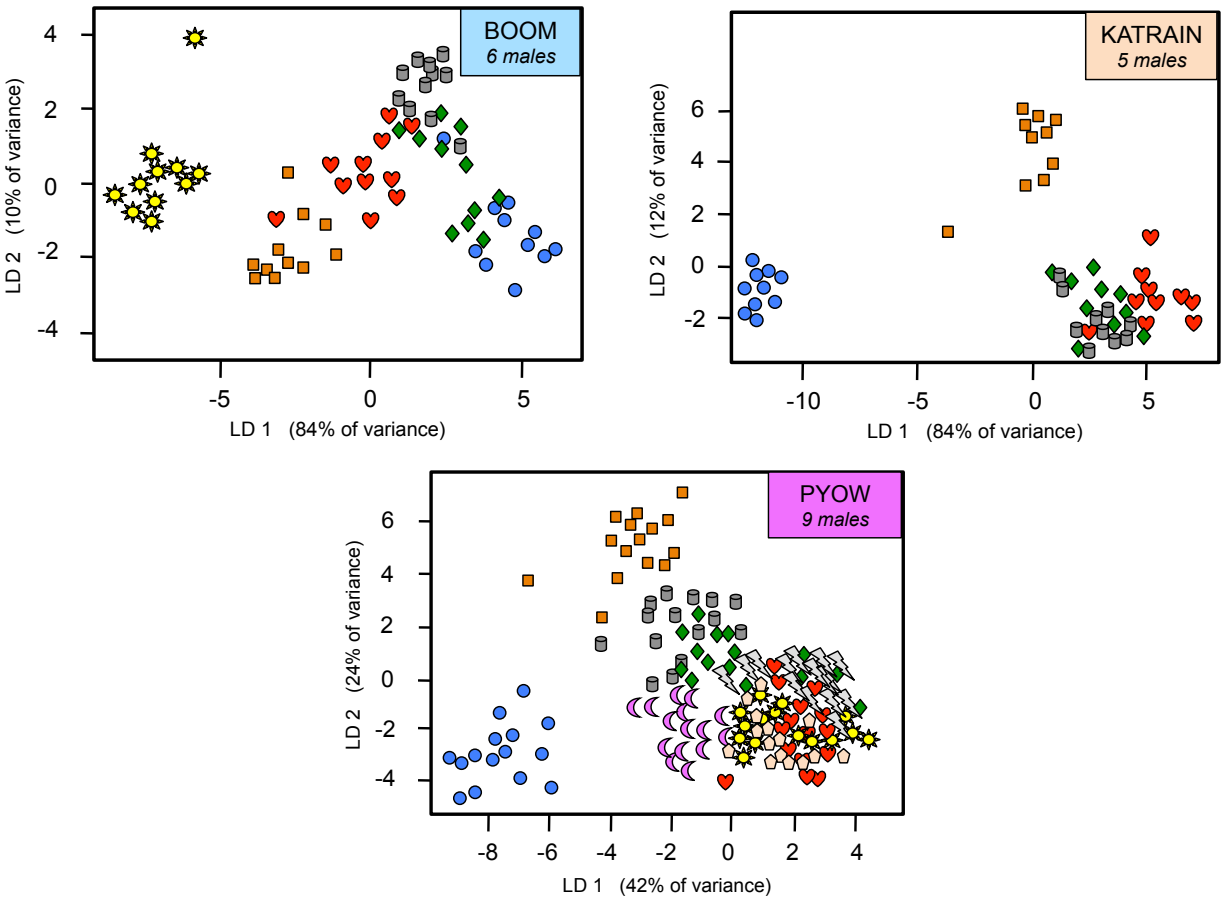

Figure 4. Results of DFA. The call samples of different individual males (symbols) are plotted along the first two linear discriminant functions.

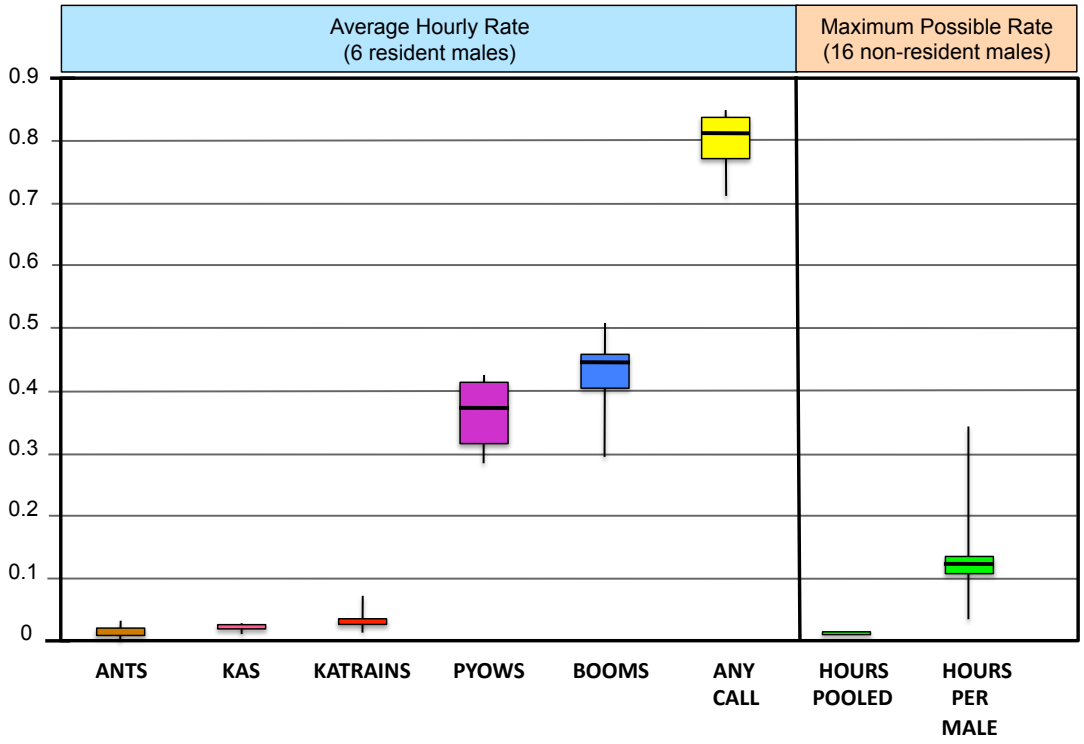

Figure 5. Left plot shows hourly usage rate for each call type, derived from mean rates of six residents. Boxes show median bound by IQR, whiskers show ranges. Right plot shows the maximum calling rate that *could* allow no calls observed for non-residents, based on all observation hours, pooled (left), and each male's hours (right).

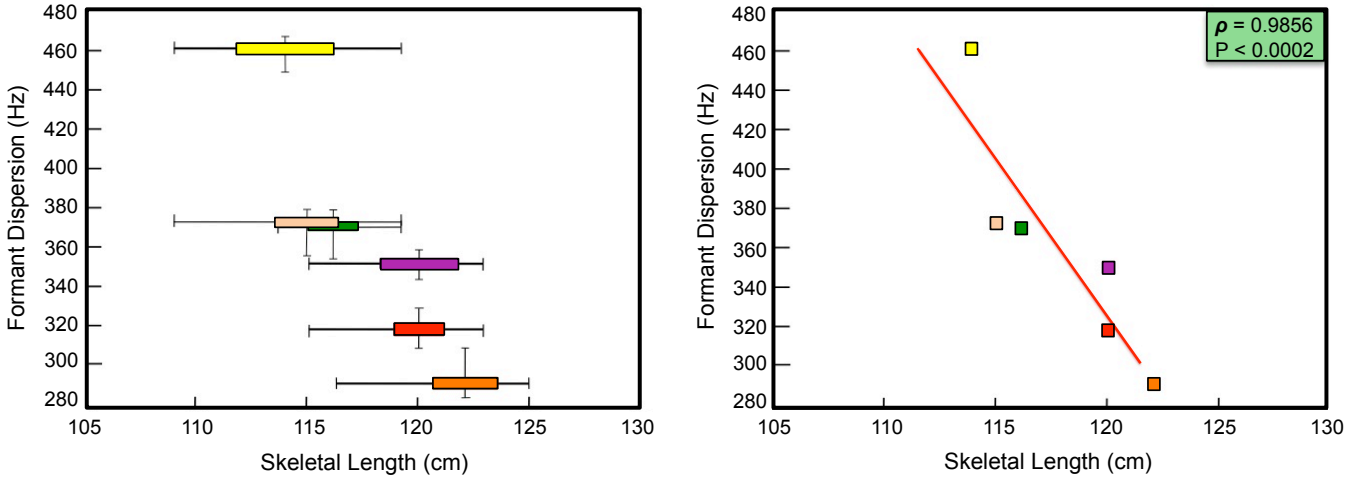

Figure 6. Skeletal length and formant dispersion for six males. Left plot shows within-subject variation in measures (boxes show one standard deviation, bisected at the mean, and whiskers show IQR). Right plot shows results of Spearman's rank correlation test (one-tailed) using mean values only.

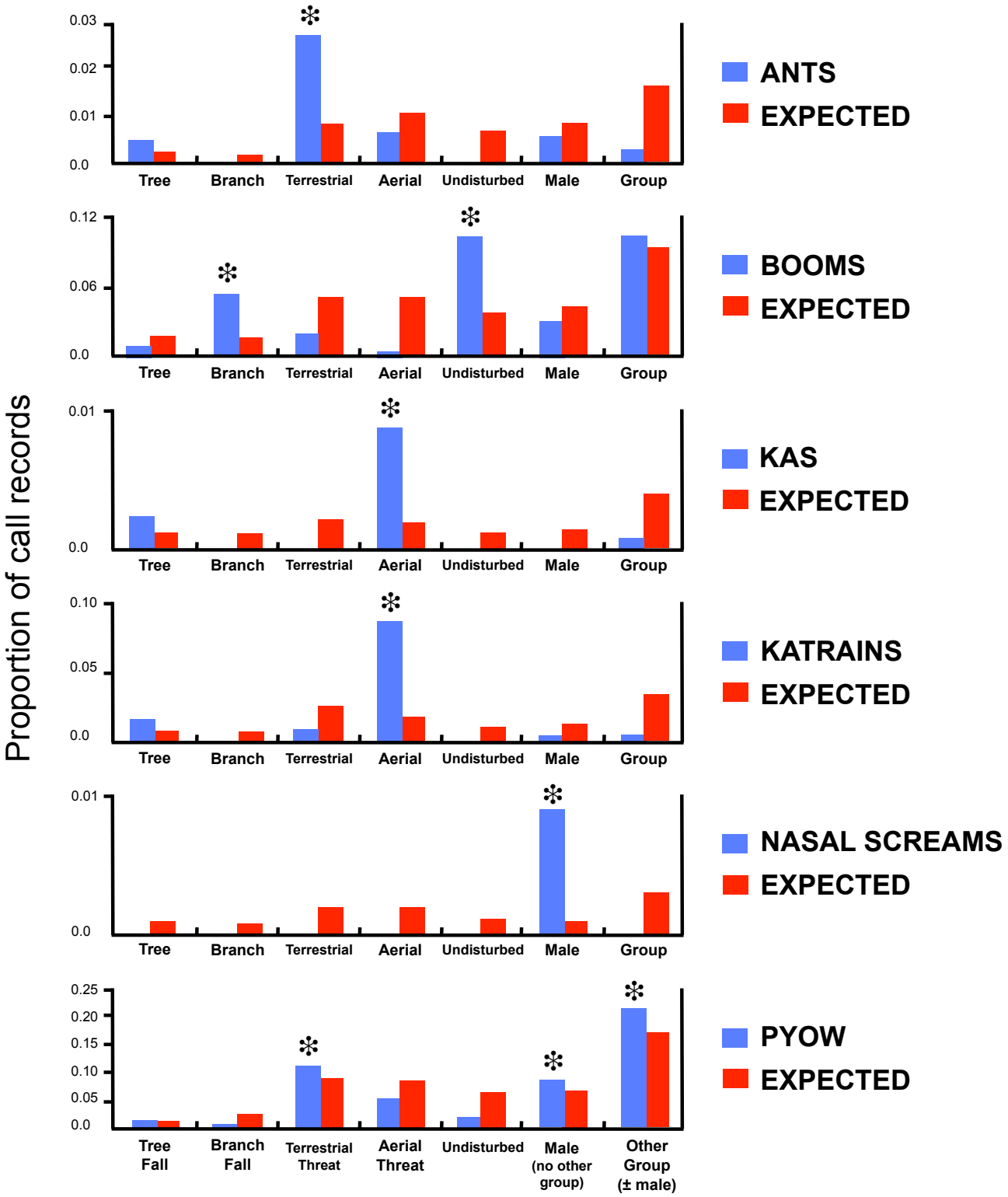

Figure 7. From natural observations, comparison of observed to expected frequencies of each call type associated with each external variable. Y-axis shows proportion of all records. Pairs marked with ❇ indicate significantly higher than expected association.

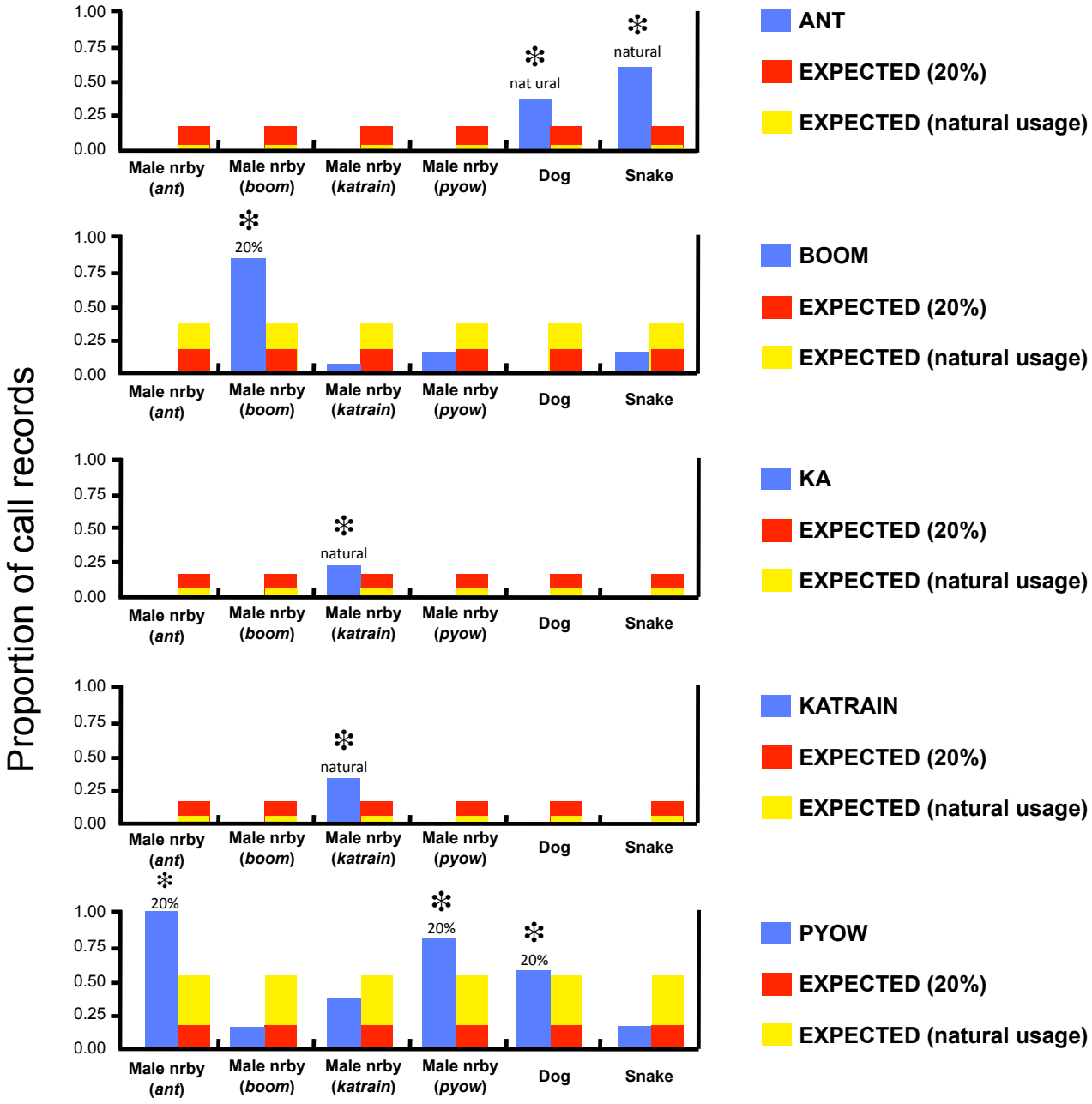

Figure 8. From stimulus trials, comparison of observed to expected frequencies of each call type associated with each stimulus. Y-axis shows proportion of trials. Expected reflect each call type's chance of occurring in a trial being 20% (red), or proportional to natural usage (yellow). Pairs marked with ❇ indicate significantly higher than expected association for either expected frequency.

CHAPTER 4

Signal function in the vocal repertoire of adult male blue monkeys (*Cercopithecus mitis stuhlmanni*).

ABSTRACT

Selection favors animals' using certain signals because they evoke responses by receivers that benefit signalers, making function (the adaptive benefit of producing a signal) essential to understanding how repertoires evolve and are maintained. During 12 months in the Kakamega Forest, Kenya, I used natural observations and playback experiments to examine the vocal behavior of adult male blue monkeys (*C. m. stuhlmanni*) and responses to their calls by males and adult females from 12 social groups and the surrounding area. Adult male blue monkeys use six distinct call types. I tested four non-exclusive functional hypotheses for each call – mate defense, mate attraction, predator avoidance, and group cohesion – by examining predictions relating to receiver response to calls, as well as variation in temporal, demographic, and contextual patterns of usage. Male blue monkey calls are loud and can be heard by multiple receivers in and outside a caller's social group; analyses therefore examined multiple receivers, differing in sex, reproductive condition, and social relationship to callers to examine the potential for calls to achieve multiple functions. Three call types (*ka*, *katrain*, and *ant*) each function in predator avoidance, with the first two relating specifically to aerial predators and the latter relating specifically to terrestrial threats such as snakes and dogs. Notably, the *katrain* also caused rival males to move away from callers, consistent with a mate

defense function. The *pyow* is best described as a general alerting signal, appearing to achieve multiple functions including repelling rival males and facilitating within-group cohesion. The *boom* has a clear role in affiliative interactions between callers and females in their groups, possibly functioning as a signal of benign intent, and was the only call type associated with proceptive interactions and an increase in number of estrous females, indicating a function in mating. Like *pyows* and *katrains*, *booms* also have a secondary function of repelling rival males. Illustrating the complex nature of selection on signal repertoires, these results indicate that call types reflect selection favoring distinctiveness in particular social and ecological contexts yet most calls appear to provide multiple benefits relating to mate defense and group cohesion.

INTRODUCTION

Across virtually every vertebrate taxonomic division, vocal communication is important in predator avoidance, reproduction, competition, and generally mediating social interactions (reviewed in Hauser 1996; Bradbury & Vehrencamp 1998; Searcy & Nowicki 2005). Understanding how signals are used, and the selection factors relating to their evolution and maintenance, therefore provides unique insight into the behavior, social dynamics, and evolution of species.

Identifying signal function (*sensu* Tinbergen 1963, i.e. reproductive or survival benefit signalers derive from producing the signal) is key to understanding how selection favors particular signal types (Dawkins & Krebs 1978). Though *vocalizing* may have inherent

benefits (e.g. in humans, laughing increases immunoglobin levels; Lambert & Lambert 1995), in the context of communication, the function of vocal *signals* is the benefit derived from receivers' responses. Such benefits may be direct or indirect (i.e. influence the reproductive success of signalers, or that of their kin or mates) and may be acquired in close temporal proximity to production or over extended periods (e.g. the predator avoidance benefits of "alarm" calls are often immediate, whereas the efficacy and benefit of signals that repel rivals may continue long after they are produced).

Animal communication research, by tradition and convention, typically examines signals in the context of exchanges between a signaler and a single receiver (Hauser 1996; Bradbury & Vehrencamp 1998; Searcy & Nowicki 2005). Though useful for empirical study, this dyadic framework typically leads to characterization of signal function based on a single class of respondent and does not address the reality that many signals, especially in highly social species, are broadcast in networks of multiple receivers (McGregor & Dabelsteen 1996; McGregor & Peake 2000) that likely differ in age, sex, reproductive state, and social status. The fitness relevance of a particular signal, and thus what constitutes an adaptive response, may therefore differ among receivers and thus predict multiple responses to the same signal. In fact, signals that evoke different responses in different receivers (and particularly the different sexes) are well known (reviewed in Berglund et al. 1996; Searcy & Nowicki 2000; Gerhardt & Huber 2002), suggesting that traditional linear models used to define "the" function of a signal are perhaps insufficient. Though selection might favor uniformity of receiver response to some signals (e.g. predator alert signals), the efficiency of signals that function in multiple capacities should also be favored.

A signal may achieve multiple functions by at least two mechanisms. One signal may simultaneously evoke different responses by different receivers; roars by male red deer (*Cervus elaphus*), for example, function in both mate attraction and mate defense by causing some rival males to retreat (Clutton-Brock & Albon 1979) or roar back if similar in size (Reby et al. 2005), whereas females may preferentially approach the caller (McComb 1991). Alternatively, a single behavioral response may confer multiple benefits. In many group living mammals, for example, some vocal signals designated "contact" or "rallying" calls have an inferred primary function of maintaining group cohesion (e.g. elephants, Poole et al. 1988; reviewed for primates in da Cahuna & Byrne 2009); far from a singular functional explanation, decreasing group spread confers a host of benefits associated with predator avoidance, resource acquisition, inter-group competition, and mating. The conspicuousness of many vocal signals, coupled with the complex social environments in which they may be broadcast, thus demands functional explanations that examine signals in the context of all receivers in signals' broadcast space and include the additive and relative influence of multiple sources of benefit.

This Study

I used a combination of natural observations and playback experiments to test functional explanations for each vocal signal in the repertoire of adult male blue monkeys (*Cercopithecus mitis stuhlmanni*). Males of this species use six acoustically distinct call types: *ant*, *boom*, *ka*, *katrain*, *pyow*, and *nasal scream* (described in Chapters 2 and 3). These signals are stereotyped, conspicuous and, with the exceptions of *nasal screams* and *ants*, audible to conspecifics at distances exceeding the average group home range length

(Brown 1989). Similarly high amplitude, species-stereotyped signals – commonly referred to as "long-distance" or "loud" calls – are described in amphibians (Gerhardt & Huber 2002), birds (Catchpole & Slater 1995), and some mammals (McComb & Reby 2009); within Primates, loud calls have been identified in nearly every genus (Gautier & Gautier 1977; Hohmann & Fruth 1995; Zimmermann 1995; Wich & Nunn 2002).

Where applicable, I inferred signal function from two types of evidence: patterns of *receiver responses* and *signal usage*. By definition, observation of consistent behavioral responses is fundamental to functional inference. In many cases, however, and especially in long-lived, socially complex species (e.g. primates), receiver responses may be facultative, individually variable, and difficult to observe, reducing the explanatory value of all but the largest samples. Testing functional hypotheses therefore often relies on other types of evidence, including contextual, spatial, and temporal patterns of usage.

Hypotheses and Predictions

Extensive research on the vocal behavior of primates has provided numerous functional explanations for different signals. Hypotheses for vocal signals of adult males, and "loud calls" in particular, typically fit one or more of four general functional categories – Predator Avoidance, Mate Defense, Mate Attraction, and Regulation of Space (Todt et al. 1987; Zuberbühler 2002; Delgado 2006). In this study, I tested predictions associated with variations on these four functional hypotheses (detailed below and in Table 1) for each signal in the repertoire of adult male blue monkeys. Importantly, I treated hypotheses as non-exclusive, allowing that some call types might serve multiple functions, and thus evaluated each hypothesis for each call type separately. Some

functional hypotheses make different predictions for behavioral responses based on characteristics of the receiver, and I therefore distinguished receivers according to sex as well as social and reproductive state (see Methods).

Predator Avoidance At least four predators of blue monkeys occur in the Kakamega Forest: snakes (e.g. Gaboon viper, *Bitis gabonica*), raptors (e.g. crowned eagle, *Stephanoaetus coronatus*), domestic dogs (*Canis lupus familiaris*), and humans (often with dogs); leopards (*Panthera pardus*) have not been observed in this forest in >10 years, but prey on blue monkeys in other parts of their range (Lawes et al. in press). The hunting strategies of these predators differ considerably, and blue monkeys likely employ avoidance behavior particular to different predator classes. I examined whether some calls function as warning signals, in general, and also whether they do so in relation to specific predator types (i.e. functionally referential signals; Marler et al. 1992).

The hypothesis that a signal functions in predator avoidance predicts its usage will be associated with the presence of predators, and that receiver response will be appropriate to the presence of predators. Receiver responses including increased vigilance behavior (e.g. scanning) and "alarm" vocalizations (note: for female blue monkeys, this putative function is assigned to distinctive *chirps* and *growls* commonly produced in predator contexts; Lawes et al. in press; M. Cords pers. comm.), and decreased group spread are consistent with a generalized response to most predators. If calls relate to specific predators (i.e. referential), call usage should correlate with detection of particular predator classes and receiver response should likewise be predator-specific (Table 1).

Mate Defense In most vertebrates, factors influencing reproductive success differ for males and females because of differential investment in offspring. Theoretically, males constrained by their access to fertile females compete with other males for mates, whereas females constrained by access to food compete with other females (Bateman 1948; Trivers 1972). As with most theoretical principles, however, nature is often more complicated than suggested and simplified classification paradigms for explaining behavioral patterns can mischaracterize natural systems (Ostfeld 1987). If a male behavior functions in repelling conspecifics from an area, for example, it can be exceptionally difficult to identify the primary benefit (e.g. mate defense or resource defense), as repelling rivals might allow exclusive access to females *and* food resources (e.g. male black and white colobus, *Colobus guereza*, actively defend both; Harris 2010). Furthermore, defending food resources may be an indirect method of gaining or maintaining access to females (e.g. in some birds, song functions to repel rival males from a territory, the resources of which in turn attract females; reviewed in Andersson 1994; Catchpole & Slater 1995). In species for which infanticide is a threat, repelling rival males may also serve to protect a male's offspring (van Schaik 2000).

In this study, I examined the hypothesis that male signals function to repel other males, with benefits likely including (but not limited to) priority of access to reproductive females and thus consistent with *mate defense*. Predictions include that call usage is associated with detection of other males, and that male receivers respond by avoiding the signaler. More generally, call usage should be correlated with the presence of estrous females and competitor males, and thus should increase during the mating season when both are more abundant (Cords 2002; Cords & Chowdhury 2010). As repelling rivals is

likely a full time concern of harem holders (i.e. resident males; see species information in Chapter 2, pp. 52), a less formal prediction would be that such calls occur "frequently."

In blue monkeys at the Kakamega Forest, infanticide by adult males accounts for at least 17% of infant mortality, and typically occurs after a new male takes over a social group (Cords & Fuller 2010). Defense against infanticide thus relates directly to resident males' reproductive success and provides another strong fitness incentive for repelling rival males; predictions relating to specifically *infanticidal* males are the same as above, except that usage would correlate with presence of infants, rather than estrous females, in the caller's group.

Mate Attraction Some vocal signals function in attracting mates in anurans (Gerhardt & Huber 2002), birds (Catchpole & Slater 1995), and some mammals (Clutton-Brock & McAuliffe 2009). This function has been suggested for many primates, though typically based on indirect or circumstantial evidence (Waser & Waser 1977; Steenbeek et al. 1999; Zuberbühler 2002; Delgado 2006), with definitive evidence of a direct relationship between vocal signals and female mate choice practically non-existent (Snowdon 2004). Difficulties in assessing the role of vocal signals in the reproductive endeavors of primates stem in part from the fact that mating decisions are likely based on numerous factors (e.g. age, size, condition, social status, and novelty of the male, as well as age, parity, status, and conceptive cycle of the female); it becomes difficult, therefore, to conclude a mate attraction function for any single behavior (e.g. producing a signal) as female response may be facultative, conditional, or delayed, and is likely interrelated with other behavior and traits of the male.

Taking a very broad view, I borrowed from Halliday's (1983) definition of mate choice as any behavior that makes the actor more likely to mate, and examined whether male vocal signals do so specifically by facilitating interactions with estrous females. Predictions stemming from this hypothesis include that signal production would be correlated with the presence of estrous females (and thus likely increase during the mating season). To definitively conclude a mate attraction function, estrous females should respond to a signal with reproductive behavior (e.g. proceptive displays, copulation); however, simply increasing proximity to the caller likely increases the probability of mating and thus may constitute indirect evidence.

Within-Group Cohesion That primate vocal signals facilitate regulation of space between individuals and groups is frequently suggested, though, as a functional category, such an explanation is exceedingly general. Repelling rival groups or males, for example, certainly constitutes regulation of space, as does attracting mates, but from an evolutionary perspective, these are better examined in terms of mating and resource benefits. For this study, I focus specifically on the ability of male vocal signals to facilitate spatial cohesion within social groups.

Permanent group living occurs across vertebrate taxa (Krause & Ruxton 2002), and is especially widespread in primates. In primates, group living is considered an adaptive response to various ecological pressures, with primary benefits of increased predator avoidance and improved resource acquisition (Wrangham 1980; van Schaik 1983; Janson & van Schaik 1988; Sterck et al. 1997), while also increasing mating opportunities and potential for cooperative care of infants (Bergmüller et al. 2007). The mechanisms by

which group living is maintained are numerous and varied; I examined whether male calls contribute by facilitating greater proximity among group members. Group cohesion is a suggested function of some primate calls, especially for species living in fission-fusion societies or in which group members are highly dispersed (Hohmann & Fruth 1995). Baboons, for example, frequently produce *barks* when traveling, a signal that functions to avoid losing group members (Byrne 1981), and chimpanzee *pant-hoots* gather others to food sites (Goodall 1986; Mitani & Nishida 1993) and into aggregations conferring benefits related to mating and defense (Wrangham & Smuts 1980).

Predictions arising from the *within-group cohesion* hypothesis include primarily that a signal evokes behavior that increases proximity among group members and to callers. Such changes would lead individuals to increase the number of neighbors they have, approaches given and received, and, possibly, affiliative or tolerant behavior (e.g. co-feeding, grooming).

METHODS

Study Site and Subjects

Fieldwork took place from September 2010 – September 2011 in the Kakamega Forest in western Kenya. Details of the study site and species information are provided in Chapter 2 (pp. 54-57), Cords (2012), and Lawes et al. (in press). Previous studies of male vocal behavior (Chapters 2 and 3) indicate that, of the six call types in the adult male repertoire, the *boom* and *pyow* are by far the most common, with the *ant*, *ka*, and *katrain* produced rarely though regularly in association with predators, and the *nasal scream*

reserved for exceptionally rare intense fights between males. Furthermore, it appears that males holding resident or influx status (i.e. occupying a heterosexual social group; below) use all call types, whereas non-resident males use only *nasal screams*.

Subjects were 32 adult males (Chapter 3, Table 1) and 62 adult (reproductive, i.e. parous or pregnant for the first time) females from 12 social groups and the surrounding area (Table 2); some data for juveniles and unhabituated females were also collected opportunistically. Subjects were unequally sampled, with most data coming from five study groups (Table 2). In these groups, all individuals were identified and well habituated to close observation, with age, parity, and maternal relatedness known. Group sizes varied between 16-50 individuals, with considerable variation within and among groups in composition of adult females (range: 7-18), juveniles (nulliparous, ≥ 2 years, either sex; median: 8; range: 4-27), and infants (< 2 years, either sex; median: 6; range: 1-12). Other social groups, peripheral to study groups and familiar to researchers at the site, were observed frequently, though their members were considerably less habituated and only the resident males were individually known. Size and composition of these groups were unknown but appeared similar to study groups.

During any observation period, I distinguished males as occupying ***resident*** (n=17), ***non-resident*** (n=16), or ***influx*** (n=10) status (status designations detailed in Chapter 2, pp. 55-56). I distinguished adult females as being ***pregnant*** (PR; pregnancy periods inferred from birth records, using estimated gestation of 176 days; Pazol et al. 2002), having a ***young infant*** <18 months old (YI) or ***no young infant*** <18 months (NYI). This distinction addresses, though imperfectly, likely differences in fitness priorities based on 1) greater vulnerability of young infants to predators and infanticide, and 2) females that

could be ovulating versus most likely anovulatory. Lacking hormonal data, I considered YI females as *probably* not ovulating based on an anovulatory post-parturition period of roughly 18 months indicated for this population by length of gestation (6 months) subtracted from interbirth interval (~24 months, when previous infant survived; Cords & Chowdhury 2010). I characterized a female as ***estrous*** in a calendar month only if she was observed to copulate or if birth records indicated she conceived then (i.e. proceptive behavior in absence of copulations did not qualify for estrus).

Data Collection

Eight trained research assistants and I (hereafter: *observers*) collected data during >10,000 man-hours of observation. For 20-22 days per month, observers followed study groups and other subjects from around 0715-1700 hrs, usually with a 90-minute break around 1230 hrs when the monkeys' were relatively inactive. Two observers normally accompanied each group, with one consistently following the resident male and the other rotating among adult females. Schedules balanced hours of observation for all subjects for times of day and per month. Non-resident males and subjects from non-study groups were followed opportunistically and when found during regular sweeps of the wider study area. I trained and supervised each observer on data collection protocols (below) and carried out frequent tests throughout the study to ensure interobserver reliability (e.g. compared data collected during mock focal samples).

Call Types

I trained observers to distinguish naturally occurring and recorded exemplars of calls until each could identify and discriminate the six male call types by ear; observation records of different calls were therefore accepted as occurrences of the standard call types described in Chapter 2. Based on interobserver reliability assessments, and the calls' acoustic distinctiveness, I am confident *booms*, *kas*, *katrains*, and *nasal screams* were never confused with other signals; likewise, the vast majority of *pyows* and *ants* were unlikely to be misidentified. Due to acoustic similarities, however, it is possible observers conflated some *ants* and *pyows*, most likely when bouts of *pyows* transitioned into *ants* (see Chapter 2). Because multiple observers were present for most loud calls, and I included only unambiguous records, however, such inaccuracies were minimal.

Call Usage

Observers collected data on male vocal behavior on an all occurrence basis (Altmann 1974) as detailed in Chapter 3 (pp. 115-117). Whenever a male vocalized, we recorded time, call type(s) and number, and caller's identity and location to the nearest 25m, using a gridded map. Observers recorded the context in which vocalizations occurred narratively, noting conspicuous social and ecological factors, callers' activity just before and after calling, and activity of other monkeys in the vicinity. Observers specifically noted the presence or absence of predators, other males, other social groups, and conspicuous disturbances (e.g. tree falls, loud human activity), and also callers' social interactions. When appropriate, I combined observations by several observers for more complete context assessment.

Guided by extensive field observations and *post hoc* examination, I categorized vocal episode records according to their agreement with several contextual variables (Table 3). Broad context categories included *Disturbances* or *Non-Disturbances*; within these two exclusive categories were nested categories (e.g. all *Snake* records were also categorized as *Predators* and *Disturbances*) that were generally though not necessarily exclusive (e.g. *Predator* events could co-occur with *Social Disturbances*).

Disturbances were associated with (i.e. call occurred within two minutes of) agonism, threats, and/or behavior indicating high arousal in caller and conspecifics, and included ecological factors (e.g. predator, tree fall) and social factors (e.g. aggression). I labeled a few episodes *Unknown Disturbance* if the caller and associated conspecifics exhibited high arousal behavior (e.g. scanning, rapid moving, vocalizing) but no particular stimulus was identified. I coded vocal behavior during playback and snake model experiments (Chapter 3, pp. 117-119) according to these same contextual variables.

Non-Disturbances were characterized by an absence of any *Disturbance* variable and behavior of the caller and nearby conspecifics generally included resting, feeding, and grooming. *Non-disturbance* contexts often included affiliative or non-aggressive interactions between the caller and group members, such as grooming or approaches. I was extremely conservative in labeling some contexts *Spontaneous*, only when no social interaction or conspicuous behavior by a nearby monkey (e.g. approaching or vocalizing while oriented toward the male) occurred in the one minute preceding the call.

Two behavioral patterns occurred frequently in both *Disturbance* and *Non-Disturbance* contexts: non-aggressive *Approach* (caller approached or was approached by another monkey from a distance of $\geq$ 5m to $\leq$ 2m and remained, without aggression, $\geq$ 5

secs) and *Rejoin Group* (caller, having been ≥ 75m from his group's edge – i.e. outermost members – for at least 20 minutes, moved directly toward group's center of mass and called upon reaching the group). I scored vocal episodes associated with these behavioral contexts in the appropriate larger context category according to other variables (e.g. an *approach* during an aggressive inter-group encounter was scored in *Social Disturbance* whereas an *approach* during affiliative interaction was scored in *Non-Disturbance*).

Receiver Response

To test predictions regarding behavioral response to vocalizations by adult males, I examined receivers' *Immediate Response* (behavior during the first three minutes after hearing call) and *Extended Response* (behavior during minutes 3-23 after call). I used data from 3- and 20-minute focal animal samples (Altmann 1974) conducted throughout the study period. For comparative analysis, I divided focal samples into *after-vocalization samples* (AVs) and *no-vocalization samples* (NVs). NVs were conducted when no male vocalization had been heard in ≥30 minutes, whereas AVs were conducted after naturally occurring vocal episodes or playbacks (samples from naturally occurring and playback calls were analyzed separately).

Playback experiments followed the methods described in Chapter 3 (pp. 117-119), and used broadcast recordings of calls (*ant, boom, katrain, pyow*) from different males and control sounds (e.g. bird calls). Each trial used recordings of males whose home range border was ≥ 500 m from that of the subject and thus all playbacks simulated "stranger" males. I did not play recordings of males to members of their own groups, as doing so required the male to be (and remain) far from the group, a condition that was rarely met.

Each female was a subject of no more than one NV and one AV per day. To compensate for the inherently smaller sample size, each male was a subject of no more than two NVs and two AVs per day. I included samples for the same subject in analyses only if separated by ≥ 3.5 hours.

3-Minute Focal Samples (Immediate Response) Observers began a 3-minute AV (ethogram in Table 4) on a receiver subject immediately upon hearing a vocalization by any adult male (naturally occurring or playback), only if no *other* male call had been heard in the previous 30 minutes. Because some behavioral responses can be extremely brief (e.g. look up), 3-minute AV samples were conducted only if the observer was looking at the subject at the exact time of the vocalization (note: this condition limited the sample size for *Immediate Responses* for naturally occurring vocalizations).

Observers recorded subjects' positions at the start of samples, including location (to nearest 25m), height from ground (estimated), distance to group's resident male, if female (*Near*, <20m, *Far*, >75m, or *Medium*), and, except for non-resident males, position relative to their social group (*In*, within an imaginary circle encompassing 75% of animals in the group, or *Edge*; occasionally, and more so for resident males, subjects were >50m beyond a ring encompassing ≥ 90% of the group, and thus labeled *Out*).

During 3-minute focal samples, observers used continuous (all-occurrence) recording (Martin & Bateson 1993) to monitor subjects' activity. Three behavioral responses were recorded only if they occurred during the first minute after hearing the call: *Look* (up, down, or toward origin of call), *Flee* (general label for unambiguous escape behavior, including run, dive, and hide), and *Collect Infant*. Throughout the entire sample,

observers recorded all occurrences of intense visual scanning, aggression (given or received), mating interaction (proceptive behavior, given or received, and mounts), displacement or self-directed behavior (scratching, auto-grooming, shaking, yawning), vocalization, and any non-aggressive approach by or of an adult male (if subject female) or any monkey (if subject male). If the subject relocated more than 5m from its start position (*Move*), observers recorded direction relative to substrate (*up* or *down*) and relative to origin of call (*toward*, *away* from, or *neutral* to).

Observers recorded subjects' location, height, and position relative to group members at the end of samples. If observers heard any male vocalization (unless by the focal subject) during an AV, or lost sight of the subject for more than a few (~5) seconds, the sample was discarded.

To measure baseline activity of subjects, observers conducted 3-minute NV samples (i.e. control samples) when no vocalization by any adult male had been heard in ≥ 30 minutes, beginning after playback of control stimuli (bird song) or by random assignment (i.e. a timer was set for 10 minutes and the sample begun on the *beep*).

20-Minute Focal Samples (Extended Response) Observers began a 20-minute AV (ethogram, Table 5) on a receiver 3-5 minutes after hearing a call by any adult male (naturally occurring or playback), only if no *other* male call had been heard >30 minutes before that call. At the start and end of samples, observers recorded subjects' location, height, and position relative to group members as described for 3-minute samples.

During 20-minute focal samples, observers used instantaneous (fixed interval time point) and one-zero (Martin & Bateson 1993) recording to monitor subjects' activity at

one-minute intervals. On each *beep*, subjects were scored in one of four mutually exclusive activity states (Moving, Feeding, Resting, or Grooming), and number of conspecific neighbors within 10m was recorded; for females, it was noted if neighbors included the group's resident male. Intervals between *beeps* were scored for any occurrence (one-zero) of the behaviors described for 3-minute samples, with the exception of *Move*.

Subjects sometimes went out of sight during 20-minute samples; when this occurred, *beeps* and intervals during their concealment were scored *OS* and excluded from analysis. If a subject was OS at the end of a sample, the sample was terminated at the time first lost. If any male vocalization (unless by focal subject) was heard during an AV, the sample was terminated immediately. Samples with fewer than 18 *beeps*, due to early termination or cumulative OS, were discarded.

To measure baseline activity, observers conducted 20-minute NV samples (i.e. control samples) when no vocalization by any adult male had been heard in ≥ 30 minutes and began after playback of control stimuli (bird song) or by random assignment. Control samples used the same protocols as AVs except that if a male subject vocalized during NVs, the sample was terminated immediately.

Some predictions required examining changes in the behavior and number of neighbors for males after *producing* (rather than hearing) a call. Observers began a 20-minute sample on a male subject 3-5 minutes after he called (*AV-Caller*), following the protocols described above.

Statistical Analyses

The following describes analyses, grouped according to particular predictions, tests, and variables. I conducted statistical analyses using R version 2.1 (R Development Core Team 2008), and tests were 2-tailed with $\alpha = 0.05$ unless otherwise specified.

Call Rate

Some predictions involved relationships between temporal or demographic variables and the rate of usage of call types. To characterize hourly usage of each call type, the unit of analysis was episodes (see Chapter 2, pp. 58) that included a particular call type (e.g. *pyow* rate was number of episodes containing at least one *pyow* per hour observed). For each calendar month, I derived hourly rates for each male subject for each call type based on the number of hours at least one observer was with him (i.e. time he *could* have been observed calling). Because some call types were rarely observed, I included data only for subjects observed >30 hours per month. To control for variation among individuals, I centered monthly call rates for each male centered around his mean (i.e. for each male for each call type, the rates used in analysis were each month's rate minus his average monthly rate for that call type).

Seasonal variation

Like most primates (Di Bitetti & Janson 2000), this population of blue monkeys exhibits reproductive seasonality, with the majority of births occurring in January-March and a corresponding concentration of conceptions in July-October (Pazol et al. 2002; Cords & Chowdhury 2010). I therefore designated January-March as *Birth* season, June-

October as *Mating* season, and other months *Off* season. The inclusion of June in *Mating* season reflects observed increases in estrus behavior prior to the peak conception period (Pazol 2003; M. Cords, pers. comm.; pers. obs.).

I compared monthly rates of usage for each call type amongst seasons using a Kruskal-Wallis one-way analysis of variance. Where differences in call rates among seasons were significant, I used a *post hoc* Nemenyi-Damico-Wolfe-Dunn (Hollander & Wolfe 1999) test to identify specific relationships.

Demographic variation

I used Spearman's correlation to examine, separately, the relationship between each call's monthly rate and the monthly number of infants and monthly total number of estrous females (i.e. number of individuals that copulated at least once) in a caller's group. To control for variation in group size among the males, I centered the monthly numbers of estrous females and infants around the mean (i.e. for each group, the values used in analysis were each month's number minus the average monthly number).

Contextual variation

Though only two hypotheses made specific predictions regarding context of usage (*Predator Avoidance* and *Mate Defense*; Table 1), I explored contextual patterns broadly to provide understanding of how different call types are used. Using call records that included clear contextual data, I examined associations within successively refined nested context categories (Table 3). To test whether call types were used in some contexts more than expected by chance, I examined each call type separately and compared observed to

expected frequencies of call-context associations; expected frequency of a call type occurring in a particular context was the proportion of all vocal episodes that included that call type times the number of episodes of that context (e.g. if 22% of all episodes were associated with predators, than 22% of all *pyows* were expected to occur in predator contexts). I used two-tailed binomial tests; because some analyses constituted repeated tests (e.g. the associations between call type and *Disturbances*, *Predators*, and *Aerial Predators*) I calculated a Bonferroni-corrected alpha.

Receiver Response

I examined receiver response to hearing each call type in separate identical analyses; naturally occurring vocalizations and playbacks were examined separately. As hypotheses make different predictions based on characteristics of receivers, I separated analyses by receivers' sex and status.

I used matched pair comparisons of AVs to NVs for individual monkeys. To ensure conditions were similar except for the occurrence of the male vocalization, AV samples were matched to NVs (hereafter: MNV or matched-NV) collected for the same individual at least one but no more than 10 days before or after, and matched for time of day (*morning*: 0700-1030 h; *midday*: 1031-1400 h; *afternoon*: >1400 h) and subjects' location relative to their group (*in*, *edge*, *out*); subjects' status (i.e. YI, NYI, PR, estrous, Resident, Non-Resident, Influx) was the same for any matched pair. For playbacks, AVs were matched to MNV-Controls (i.e. playbacks of bird song).

Male Receivers The only prediction relating to behavioral responses of male receivers is that they will avoid callers after hearing a call (*Mate Defense* hypothesis; Table 1), making receivers' movement relative to a caller the only variable of interest. I examined responses by Resident and Non-Resident males separately (Influx males were excluded due to inadequate AV sample sizes), and distinguished AVs based on the distance between caller and receiver.

For all AV and MNV samples, I first derived subjects' *Distance Traveled*, in meters, using location at beginning and end of samples; because location was given as nearest point on a grid, net movement <25m was not examined. For all AVs, I scored receivers' movement in relation to call origin (MRC) as *Toward* (receiver closer to call origin at end of sample), *Away*, or *Neutral*; for playbacks, including MNV-controls, MRC was derived in relation to the speaker.

I tested whether male receivers traveled more (in any direction) after hearing a call by comparing *Distance Traveled* in AVs and MNVs using Wilcoxon matched-pair signed rank tests. I also tested if the distance traveled after hearing a call (i.e. during AVs only) was correlated with subjects' distance from the caller, using Spearman's rank correlation.

To test whether receivers avoided the location of a call's origin, I used two approaches. In comparison of playback AVs to MNV-Control samples, I used Fisher's exact tests to compare frequencies of different MRC categories (*Toward, Away, Neutral*). Naturally occurring AVs lacked a control for comparison (i.e. MNVs had no call origin to move toward or away from); I therefore tested whether male receivers' MRC *Away* was greater than expected by chance. Taking the subset of samples in which the receiver moved ≥25m, I compared the observed frequencies of MRC *Away* and MRC *Toward*

using a two-tailed binomial test; this comparison assumed that random movement is equally likely to be in any direction relative to a caller.

Callers To examine the hypothesis that receivers in a caller's group increase proximity to a caller after he calls (see also *Female Receivers*, below), I compared males' 20-minute focal samples after he had called to those when he had not (i.e. AV-Callers to MNVs). I examined, separately, the total number of *beeps* (i.e. proportion of sample) with any neighbors, as well as *beeps* in different ordinal categories of number of neighbors (1-2, 3-4, and >4). Similarly, I compared number of *beep* intervals during which a male approached or was approached by conspecifics (Table 14, Figs 11, 12). Each analysis used a Wilcoxon matched-pair signed rank test, with a Bonferroni corrected alpha level of 0.008 (i.e. 0.05 divided by 6) to address the variables' non-independence.

Female Receivers To test whether female subjects' activity changed after hearing a call, I compared AV and MNV samples for each call type using logistic regressions with the variable *Stimulus* (i.e. heard call or did not hear call) as the binomial dependent variable and particular activities of subjects as independent variables. This arrangement reverses conventional labeling of predictor and response variables yet, as regression analyses are correlational by nature, poses no theoretical or mathematical constraints on interpreting results; resultant odds ratios indicate the likelihood a change in a given activity is associated with having heard a call.

For each call type, I ran a generalized linear model (GLM) with data from AV-MNV pairs; because female response likely relates to her relationship to the male, I used AVs only in which the caller was the resident male of the subject's group (*familiar*). GLMs included values for activities recorded during 20-minute focal samples (Table 5), including the derived measures *Distance Traveled* (described above) and *Change Relative to Male* (*Closer*, *Farther*, or *Same*; this variable, conceptually similar to MRC, above, compared subjects' location relative to the resident male at the start and end of samples and thus allowed comparison between AVs and MNVs). To examine whether estrous females responded differently to calls, I ran separate analyses with only estrous females, only non-estrous, and all females pooled.

In addition to females' extended response (above), I examined immediate responses using records for 3-minute AV samples. Here, I included AVs for which the caller was in the subject's same group or a different group (*stranger*), but included records only for which callers were <100m away. I separated analyses based on subjects' social relationship to callers (i.e. same or different group), and also for playbacks and naturally occurring calls. To control for differences among subjects, I balanced the number of responses to each call type for any individual (i.e. each female's number of responses to *pyows* was equal for *booms* and *katrains*, with records matched to within 20 days). I tested whether subjects' response to hearing a call differed among call types by examining differences in nine behavioral responses (Table 4). I used Fisher's exact tests to determine whether receivers' likelihood of exhibiting predator specific responses (look up or down, move up or down, flee), alarm vocalizations (*chirps* and *growls*), vigilance scanning, or proceptive interactions differed among call types. This same approach, using

separate analyses with only females who had infants, was used to test whether call type affected the likelihood mothers collected their infants.

RESULTS

Call Usage

For five resident males, hourly rates of calling, calculated for each month, varied both among and within individuals, yet the pattern of near-daily *booms* and *pyows* and more rare *ants*, *kas*, and *katrains* was general to all males (see Chapter 3, p. 131) and throughout the year. Because *nasal screams* were extremely rare (only 11 episodes observed during the study), I did not include data for *nasal screams* in statistical analyses; qualitative description is provided below and in the Discussion.

Seasonal and Demographic Variation

Among the five resident males, only *pyows* showed significant seasonal variation in rate of usage (Kruskal-Wallis H = 10.3638, $p = 0.0056$). Males' hourly rate of *pyows* was higher during Mating season than Birth season (Nemenyi-Damico-Wolfe-Dunn test, p=0.003) and did not differ during Birth and Off seasons; though *pyow* rate appeared higher during Mating than Off season, this difference was not significant (Table 6, Fig 1).

Number of Estrous Females In the five primary study groups, females copulated throughout the year, though there were typically more estrous females in groups during July and August (peak Mating season; Fig 2). Only the rate of *booms* showed a

significant relationship with number of estrous females, with hourly rate increasing in months when more females were estrous (Spearman's rank correlation, rho=0.6043, n=5, p <0.0001; Table 7, Fig 3).

Infants I used two separate analyses to compare monthly call rates and the number of infants in a group each month. I used the total number of monkeys 24 months old or younger (*All Infants*) and then only those ≤ 18 months (*Young Infants*). In each of the five primary study groups, infants were present throughout the year, peaking (especially for *Young*) during the Birth season (Fig 4). No call type's rate showed a significant relationship with the number of infants in groups (Spearman's rank correlation, Table 8).

Contextual Variation

Of the >10000 call records collected during the study period, nearly 60% were for males not seen when they called (i.e. distant callers or focal males gone out of sight). To characterize contextual usage of each call type, I examined only records of vocal episodes that included observed callers and for which observations included data sufficient to unambiguously assess context (n=3384).

For records of each of the five call types, I conducted six binomial tests (Tables 9-12), with the Bonferroni corrected alpha level of 0.008 (i.e. 0.05 divided by 6). *Booms* occurred equally in *Disturbance* and *Non-Disturbance* contexts, which was less in *Disturbances* than expected by chance. All other call types occurred more in *Disturbance* contexts than expected (Table 9, Fig 5) – nearly 80% of *pyows* and 100% of *ants*, *kas*, and *katrains* (binomial test, $p < 0.008$).

For calls produced in ***Predator*** contexts (all predator classes pooled; n=657), the proportions of *ants*, *kas*, and *katrains* were each greater than expected by chance and the proportion of *booms* was lower than expected; the proportion of *pyows* occurring with any predator was not significantly higher than expected ($p=0.009$; $\alpha = 0.008$). For aerial predator events only (n=241), *booms* and *pyows* occurred less than expected by chance, whereas *kas* and *katrains* each occurred more than expected; the proportion of *ants* did not differ from expected. For terrestrial predators (n=371), *ants* and *pyows* were each associated more than expected, whereas *booms* were associated less than expected; the proportions of *kas* and *katrains* did not differ from expected (Table 10, Fig 6; binomial test, $\alpha = 0.008$).

In vocal episodes involving ***Male agonism*** contexts (n=687, *pyows* were associated significantly more than expected by chance. All other call types were associated with male agonism less than expected, though the relationship with *ants* was not significant (Table 11, Fig 7; binomial test, $\alpha = 0.008$).

In vocal episodes involving non-aggressive ***Approaches*** (i.e. a caller approached or was approached by other monkeys; n=861), *booms* were associated more than expected by chance and, notably, were associated with 92% of approach contexts in which males vocalized. The other call types were associated with *Approaches* less than expected, with *kas* and *katrains* never associated with approaches and *ants* only once (Table 12, Fig 8; binomial test, $p < 0.008$).

Receiver Response

Table 13 summarizes records of focal samples used in examining receiver response to male calls. Analyses were limited to *booms*, *pyows* and *katrains*; low sample sizes for AVs following episodes of only *ants* or *kas* precluded meaningful analyses for these call types. Analyses for *booms* and *pyows* included episodes in which only the one call type was produced; as naturally occurring *katrains* commonly co-occur with one or more *kas*, however, such episodes were included and not distinguished. For non-resident males, focal samples after hearing *booms* were practically non-existent (and thus excluded), reflecting smaller observation times and also the tendency of non-residents to be far from residents, rendering most *booms* inaudible to observers.

Male Receivers

Non-Resident Males Compared to after *not* hearing a call, non-residents traveled farther during 20-minute samples after hearing *pyows* (Wilcoxon signed rank, W=753, n=15 males in 72 AVs, p=0.016) or *katrains* (W=0, n=8 males in 11 AVs, p=0.0089; Fig 9). The distance traveled after a *pyow* was greater when the caller was closer (Spearman's rank correlation: rho=-0.2414, p=0.034); the same relationship was not significant after *katrains* (Spearman's rank correlation: rho=-0.3676, p=0.3305). When subjects moved at least 25m after hearing a call, they were much more likely to move away from the call origin (*pyows*, n=37 AVs: *Away*: 71%; *Toward*: 9%; binomial test, p<0.0001; *katrains*, n= 9 AVs: *Away*: 100%; binomial test, p<0.0001).

After playbacks of *pyows* or *katrains*, non-residents never moved toward the speaker and moved away more often than they moved neutral or remained still. This pattern,

however, was not significantly different from when control bird song was played, either for *pyows* (males moved away in 4 of 6 trials vs. 0 of 6 control trials; Fisher's exact test: p=0.061) or *katrains* (males moved away in 4 of 8 trials vs. 1 of 8 control trials; Fisher's exact test: p=0.281).

Resident Males Compared to after *not* hearing a call, residents traveled farther during 20-minute samples after hearing *booms* (Wilcoxon signed rank, W=3927, n=8 males in 150 AVs, p=0.0263) or *pyows* (Wilcoxon signed rank, W=26243, n=9 males in 465 AVs, p=0.0003); travel after hearing *katrains* did not differ from MNVs (Wilcoxon signed rank, W=127.5, n=7 males in 57 AVs, p=0.0704); Fig. 10). The distance traveled after hearing a call was not influenced by distance to the caller (Spearman's rank correlation: *booms*, rho=0.051, p=0.535; *pyows*, rho= 0.067, p=0.180; *katrains*, rho= 0.095, p= 0.483). When subjects moved at least 25m after hearing a call, it was more likely to be away if the call was a *boom* (*Away*: 72%; *Toward*: 25%; binomial test, p<0.0001, n=82); after hearing either *pyows* (n=329) or *katrains* (n=28), likelihoods of moving away from or toward the caller were not different (binomial test, p=0.5064 and 0.5413, respectively).

After playbacks of *katrains* (n=6), residents moved away from the speaker 83% of the time, but this was not significantly different from the 33% that did after control bird song (Fisher's exact test: p=0.242). After *booms* or *pyows* were played (n=5, n=7, respectively), subjects were more likely to change their distance to the speaker than after controls (Fisher's exact test, p=0.048 and p=0.011, respectively), yet likelihoods of moving toward or away from "callers" were practically the same (*booms*, Away: 40%, Toward: 40%; *pyows*, Away: 29%, Toward: 43%).

Though not relevant to any specific hypothesis, it is worth noting that response by adult males (resident and non-resident) to hearing calls never resembled anti-predator behavior; they did not dive down or hide and, when moving away, tended to do so gradually and often at the same height. This observation is in marked contrast to female response (below), especially to hearing *katrains*.

After Calling

To test whether female receivers increased proximity to a male after he called, I compared males' time spent with neighbors (conspecifics within 10m), number of neighbors, and number of approaches received or given during 20-minute AV-Caller and MNV samples (Table 14, Figs. 11, 12).

Compared to after not calling, males spent more time with neighbors after producing either *booms* (n=13 males in 628 AV-MNV pairs; Wilcoxon signed rank test, W=97928, $p < 0.0001$) or *pyows* (n=7 males in 506 AV-MNV pairs; W=72901.5, $p < 0.0001$). Time spent with 1-2 neighbors did not differ after calling, but time with 3-4 and >4 neighbors was greater after calling. Males received more approaches after *booming* than after not calling (Wilcoxon signed rank test, W=17332, $p < 0.002$), though rate of approaching others did not change. The increase in approaches received after *pyows* was not significant at the 0.008 level (Wilcoxon signed rank test, W=1460.5, $p = 0.014$).

The number of AV-Caller samples for other call types was too low for meaningful analyses. This shortfall reflects both the relative rareness of *ants*, *kas*, and *katrains*, as well as these calls' associations with predators and thus a tendency for several different males to vocalize within a short time (precluding AV samples). Though drawing

inferences is therefore not advised, I compared the number of neighbors and approaches before and after *ants* and *katrains*, without any statistical test. The pattern of time with neighbors after *katrains* appears generally similar to that for *booms* and *pyows* (greater after calling), whereas the number of approaches received appears less after calling. After *ants*, males appear to have spent less time with neighbors and to have been approached less (Table 14, Figs. 11, 12).

Female Receivers

For female receivers, I tested whether behavior exhibited in the first three minutes after a call was independent of call type. Responses differed among calls, and patterns were similar whether caller was the subject's resident male (*familiar*; n=228) or from a different group (*stranger*; n=189; Table 15); results of playbacks, simulating stranger males, did not differ from those of natural stranger male records, and I report results of pooled analyses only.

Females' likelihood of *Moving Down*, *Fleeing*, *Growling*, and *Scanning* was related to call type, whether the caller was the subject's own resident male or not (Fisher's exact test; $p < 0.01$; Table 15), as was the likelihood of producing *Chirps*, though only when the caller was familiar (Fisher's exact test, $p=0.002$). Post hoc 2x2 Fisher's exact tests indicated that, with familiar callers, each of these behavioral responses was higher after *katrains* than either of the other call types. Similarly, when the caller was a stranger, *Growling* and *Fleeing* were more likely after *katrains*, as was *Moving Down*, though the latter only relative to *pyows* (i.e. likelihood of moving down did not differ between

booms and *katrains*). When the caller was a stranger, *Scanning* was lower after *booms* than other call types (Table 15).

In examining females' extended response to hearing a call, I restricted analyses of 20-min AV samples to cases in which the caller was the resident male of the subject's own group. Females' activity after a call differed from when no call was heard, and responses differed among call types (Table 16). Results for estrous females did not differ from those of anestrous females, and I therefore report results of pooled analyses only.

After hearing *booms*, females (n=61 in 663 AV-MNV pairs) were more likely to move toward (and thus less likely to move neutral to) the caller, and also spent more time in proximity and had more proceptive interactions with the caller than when he had not called (GLM, $p<0.02$). After hearing *pyows*, females (n=61 in 603 AV-MNV pairs) traveled farther, and were more likely to move in the direction of the male (GLM, $p<0.02$), but did not change time spent ≤ 10m of him or other group members. After *katrains*, total time spent with neighbors did not change (GLM, $p=0.318$), but females spent more time with greater numbers of neighbors ($p<0.001$) and more time scanning than when no call was heard ($p<0.001$).

Nasal Scream

Observations of *nasal screams* were exceptionally rare: only 11 records over the entire year, of which seven were closely observed. There was an apparent association with *nasal screams* and the mating season, consistent with an increased presence of males in and around social groups; notably, the call was observed predominantly in groups experiencing multi-male influxes and thus associated with an increase in male-male

interactions. Consistent with observations over several decades (M. Cords, pers. comm.), observed cases occurred during aggressive interactions that included physical contact or, with other males in extreme proximity, when such contact appeared imminent. In all observations, only the recipient of the aggression (i.e. the putative "loser") *nasal screamed*, and in two cases during fights in which he sustained severe wounds to the face and wrists. In three of the four cases in which the caller was not directly observed, he had been out of sight for a few minutes only, with aggression between two males observed just before or just after the call. In one case, a male went out of sight while being chased and harassed by several adult females and was heard *nasal screaming* shortly afterwards.

DISCUSSION

The results of this study clearly support several functional hypotheses for the different signals of the adult male blue monkey vocal repertoire. Notably, some signals achieve multiple functions, and some functional explanations are shared across signals, illustrating the complicated and dynamic nature of selection on this communication system. Results indicate that each call type can be described by a "primary" function relating to aerial predators (*katrain* and *ka*), terrestrial predators (*ant*), repelling rival males (*pyow*), or attracting females (*boom*), yet most calls appear to provide multiple benefits relating to mate defense and group cohesion. The following, including the summary Table 17, discusses results for each call type in relation to support for the proposed functional hypotheses.

Boom

The *boom* was the most commonly used call of the male repertoire, with a resident male typically producing about three *booms* during an all day observation period. Based on the auditory ability of *C. mitis* and the call's acoustic structure and amplitude, Brown (1989) calculated that *booms* are likely audible to conspecifics nearly a kilometer away; their low frequency and structure (Chapter 2), however, make *booms* difficult for human observers to hear, even sometimes from as close as 50m, potentially leading to underestimation of both their rate of occurrence and potential role in long distance communication.

The results presented here provide strong evidence of a relationship between *booms* and mating. Unlike any of the other call types, the rate of *booms* was positively correlated with the number of estrous females in a caller's group (Fig 3). Though the lack of increase in *booms* during the mating season (Table 6) appears at odds with this finding, females copulated during every month of the study period, with at least seven conceptions (in three groups) occurring during the "birth" season (Fig 2). The strong seasonality in births (and thus mating) identified for this population by Cords and Chowdhury (2010) reflects nearly 30 years of observations and a sample size large enough that variation at more refined scales (e.g. the 12-month period of my study) are absorbed into a clear seasonal pattern.

The response by female receivers was also consistent with, and more indicative of, a mate attraction function. After *booming*, males spent more time with more females than after not calling, and were more likely to be approached, and, crucially, to mount or receive proceptive displays (Tables 14, 16). The unexpected result that females' response

did not appear to depend on their being estrous possibly suggests other benefits of attracting neighbors (i.e. group cohesion hypothesis), though it might simply reflect an overly conservative approach to labeling estrus.

The association between *booms* and non-aggressive approaches (Fig. 8) was extremely strong, and nearly half of all observed *booms* were immediately preceded by a caller's approaching or being approached by females (Table 12). Along with the observations that males spent more time in proximity to females (above) and were more likely to be groomed or to co-sit with females (data not reported) after *booming*, these results indicate a role in facilitating affiliative interactions consistent with the *boom* as a signal of *benign intent* (*sensu* Silk 2002). As Silk (2002) summarized, the rate of "unprovoked" aggression among group mates is high in many primate species, a pattern that predicts animals might *always* try to avoid potential aggressors and thus questions how "friendly" associations are maintained. In several primates, the use of signals specifically associated with non-aggression appears to provide answers, with signalers less likely to behave aggressively and receivers less likely to retreat afterward (e.g. rhesus macaques, chacma baboons, reviewed in Silk 2002; chimpanzees, Waller & Dunbar 2005). Observations of *booms* appear especially similar to the pattern observed in chacma baboons by Palombit et al. (1999), in which males that *grunted* when approaching females were more likely to enjoy affinitive interactions than when they did not *grunt*.

Though not associated with any of the stated predictions of this study, a pattern of *booms* being given in response to *long grunts* (syn: *croak*, Tsingalia & Rowell 1984; distinctive long, low-frequency signals used by females) is so striking as to warrant attention. *Long grunts*, apparently given exclusively by adult females, are almost never

observed in any context other than when a female is near or interacting with males, and most frequently occur when he is approaching or being approached (unpublished data). That *booms* often follow females' *long grunts* has been noted by others (Tsingalia & Rowell 1984; M. Cords, pers. comm.) and was observed during this study with such consistency that field assistants reported the ability to "predict" *booms* from hearing *long grunts*. There is a very strong impression that *long grunts* somehow solicit *booms*; females, even in the absence of approaches, often produce increasingly louder and longer *long grunts* until a male *booms*, and then cease immediately. Tsingalia and Rowell (1984) noted that it was sexually receptive females in particular that *long grunted* when approaching males, potentially similar to estrous female brown capuchin monkeys (*Cebus apella*) that continuously follow males and make distinctive loud vocalizations when approaching (Janson 1984).

The *boom's* association with social interactions between a caller and group members might explain why *booms* occurred across such a wide variety of contexts (i.e. non-aggressive interactions with females may be equally beneficial during predator events, aggressive intergroup encounters, or in peaceful contexts). With such strong evidence of the *boom's* affiliative function, however, the predictability with which *booms* were given after tree branches fell (Chapter 3, p. 133) remains perplexing. When males produced a vocal signal in response to a branch falling nearby, it was a *boom* more than 80% of the time, a seemingly reflexive response that did not appear to depend on the behavior or even presence of nearby females. No functional explanation relating to branches falling seems readily apparent, and it may simply reflect a non-adaptive behavior with little selection against it. If one were given to speculation, however, the tendency for adult

males to break branches during aggressive displays to other males (pers. obs.) might suggest a spillover from selection favoring a rival repelling function.

Evidence of the *boom's* function in facilitating affiliative interactions and mating opportunities is strong, yet a question lingers: why so loud? Signals of benign intent described in other species (above) tend to be quiet calls or facial gestures, unlikely to be perceived by animals outside the immediate proximity of the signaler. The blue monkey *boom*, however, has an extremely long audible distance (potentially as great as 900m; Brown 1989), seemingly incongruent with observations that the evoking stimulus (i.e. solicitous females) is only a few meters away. Furthermore, *booms* rely on specialized supralaryngeal anatomy (Gautier 1971) and, relative to some other primates, blue monkeys exhibit superior hearing of low frequency sounds (Brown & Waser 1984); no benefits beyond the producing and perceiving of this one call type have been suggested for these specializations.

At least two non-exclusive hypotheses are consistent with the *boom's* loudness and its clear role in affiliative interactions with nearby females. It is possible that, like many sexually selected traits (reviewed in Andersson 1994), the *boom* reflects selection pressure from females' responding preferentially to signals that are especially costly (i.e. handicap principal, Zahavi 1975) or relate to some feature of male reproductive quality (e.g. energetic condition) that a quieter call could not convey. Secondly, the *boom* might provide benefit by also repelling rival males, a function whose fitness relevance is greater when receptive females are present. That the *boom's* audible distance surpasses the extent of a caller's social group's territory is consistent with a mate defense function (Mitani & Stuht 1998; Wich & Nunn 2002). To conclude this function, however, requires evidence

that rivals actively avoid callers after *booms*. That resident males tend to move away from callers after hearing booms (Fig 10) certainly supports this conclusion, but further study is necessary to determine how non-residents respond.

Pyow

The *pyow* was the second most commonly produced call type, with a resident male producing two-to-three *pyow* bouts typically during an all day observation period. With an estimated audible distance greater than one kilometer (Brown 1989), acoustic energy that is broadly distributed, and a tendency to be repeated in bouts of three to four calls (Chapter 2, pp. 75-76), most human observers find the *pyow* is generally the most familiar and easily detected male call.

The *pyow* occurred across a wide variety of contexts and in association with extremely varied stimuli, including predators, other males, within-group aggression, and often with no apparent cause (i.e. "spontaneous"). Despite the strong impression of being a "generalist" signal, however, the evidence of a primary benefit relating to repelling rivals is quite strong. The *pyow* was the only call type to show significant seasonal variation, occurring more often during the mating season (Table 6, Fig. 1). Though this appears consistent with a mate attraction function, the lack of association with the number of estrous females (Table 7) suggests the increase in *pyow* rate may instead relate to increased presence of other males; though not examined directly for this study, the number of males seen near groups appeared higher during the mating season, consistent with a pattern identified by Tsingalia & Rowell (1984) and Cords (2002).

The *pyow* was the only call type positively associated with encounters with other

males, with 30% of all *pyows* occurring during agonistic interactions between males (Table 11, Fig 7); this figure is likely quite conservative, as solitary males are often difficult to see and some *pyows* labeled *unknown disturbance* probably also related to other males nearby. *Pyows* were frequently given "in response" to hearing calls by other males, whether naturally occurring or playback, a pattern that Butynski (1982) suggested provides opportunity for male rivals to both regulate spacing and also assess callers' "quality" (i.e. attributes relating to competition, such as body size, status, identity; Chapter 3). A similar assessment function is suggested to explain counter calling in many vertebrate taxa (Bradbury & Vehrencamp 1998), yet is rarely evaluated systematically; in guereza monkeys (*Colobus guereza*), however, Harris (2005) showed that male roaring behavior related to callers' willingness and ability to defend mates and food resources.

The response by non-resident males – typically moving farther and away from callers after *pyows* (Fig 9) – provides the most definitive evidence of the *pyow's* function in repelling rivals. As non-residents are a significant threat to residents' reproductive success – directly ousting them or stealing paternity through "sneak" copulations (Tsingalia & Rowell 1983; Cords 2000) – repelling non-residents is undeniably important. In light of the avoidant response by non-resident males, the *pyow's* audible distance being well beyond the home range of the caller and his group (Brown 1989) provides more support, though indirect, for a mate defense function. Though male loud calls function to attract distant females in numerous taxa (e.g. birds; Searcy & Andersson 1986), female blue monkeys are strictly philopatric (Cords & Chowdhury 2010) and aggressively defend their territory against incursion by non-group females (Lawes & Henzi 1995; Cords 2007), suggesting that the response most relevant to callers is that of

other males. Lastly, given that threats posed by other males in terms of infanticide, mate competition, and loss of residency are likely continuous concerns for residents, the frequent, and sometimes "spontaneous" use of *pyows* – consistent with the call's being a general advertisement of occupancy – also supports a rival repelling function.

Several authors have stated that the *pyow* functions as an intragroup rallying call (Butynski 1982; Tsingalia & Rowell 1984; Lawes et al. in press), though it appears the research presented here constitutes the first systematic evaluation of this hypothesis. Results are consistent with the group cohesion hypothesis, with females tending to move toward the caller, and spending more time with more neighbors and the caller after hearing *pyows* (Table 16, Fig 11). Observations that males frequently *pyowed* when outside the group or upon returning to the group (data not reported) are also consistent with this function. Though maintaining proximity to females undoubtedly improves a caller's likelihood of mating, the *pyow's* lack of association with estrous females (Table 7) and the fact that proceptive interactions did not increase after *pyows* (Table 16) suggests primary benefits relate more broadly to group cohesion (e.g. predator avoidance, resource acquisition, mate monopolization).

Pyows were given in practically every context, and appeared to be evoked by an array of stimuli that defied categorization by including predators, other males, tree falls, within-group aggression, group travel, and even the peaceful quiet of apparently nothing at all. With at least some support for each of the hypotheses evaluated in this study, the *pyow's* functional versatility might be best explained if a singular function is common to several hypotheses. For example, though *pyows* showed a significant association with terrestrial predators, and dogs in particular (Table 10), the call's association with so many

other contexts (70% were *not* to predators) makes it inappropriate to characterize it as a predator alarm (discussed in Chapter 3). A signal that functions "simply" to alert group mates and attract movement toward the caller, however, is likely of benefit in some predator events, when rival males are nearby, or when moving toward a new foraging area. Furthermore, the variety of evoking stimuli (consistent with many other primates' use of a "general alarm" call associated with terrestrial predators, loud noises, and intergroup aggression; e.g. lemurs, Fichtel & Kappeler, 2002; white-faced capuchins, Digweed et al. 2005) provides a convenient proximate mechanism by which dual ultimate functions of repelling rivals and facilitating group cohesion could be maintained.

Katrain

The extreme consistency with which *katrains* were associated with predators (Table 10) demonstrates the call's clear role as a predator alarm. *Katrains* were tied specifically to aerial threats, with birds of prey, and an occasional low-flying airplane, associated with 70% of all observed *katrain* episodes (note: this measure is actually conservative, and at least some of the 19% of *katrains* labeled *unknown predator* or *unknown disturbance* were undoubtedly also linked to aerial threats). This pattern is extremely similar to that seen in the closely related putty-nosed monkey (*C. nictitans*), which use *hacks* (an abrupt call structurally similar to blue monkeys' *ka*) in association with eagles (Arnold & Zuberbühler 2005).

Behavioral responses by females were consistent with predator-avoidance, in general, and aerial predators in particular (Tables 14, 15, 16). Upon hearing *katrains* (natural or playback), female receivers were more likely to flee and produce *chirps* and *growls*, and

also spent more time scanning and in close proximity to more monkeys. These responses likely confer a variety of predator avoidance benefits, namely increasing the potential for cooperative defense (e.g. mobbing; Curio 1978), vigilance ("many eyes" hypothesis), dilution (i.e. individuals reduce their odds of being killed by being near other potential prey; Bertram 1978), and predator confusion (Milinski & Heller 1978). Consistent with an *aerial* predator response (Seyfarth et al. 1980), females were significantly more likely to move down after hearing *katrains* than other call types; the likelihood of looking up was twice that of other calls, yet this pattern was not significant ($p=0.068$). The specificity of use and consistency of female responses indicates the *katrain* is a functionally referential signal (Evans 1997; Seyfarth & Cheney 2003), suggesting a high level of selection on both signaler and receiver. That blue monkeys have evolved a signal-response pattern specific to aerial predators suggests that, for this species (or somewhere in its evolutionary history), the benefit of avoiding raptors (or, conversely, the fitness consequences of *not* doing so) is considerable.

Katrains were occasionally produced in response to other disturbances, including nearby falling trees, dogs, and loud vehicles. Though none of these constituted a significant association, it is notable that when males *katrained* at such things, it appeared that the close proximity of the disturbance to the caller, rather than some intrinsic characteristic of the disturbing entity, predicted the call. Producing signals considered "predator alarms" in the absence of predators is often referred to as a "mistake" (e.g. Hollén & Radford 2009). Though intuitive and convenient, this appellation makes more presumptions about the mechanisms by which signals operate (e.g. that there is a "correct" form to which animal behavior should adhere) than this paper has room to

address. From an evolutionary perspective, however, it is perhaps informative that the non-raptor stimuli that evoke *katrains* appear associated with sudden, extreme spikes in callers' arousal. Such an observation is difficult to reconcile with a semantic view of signaling (i.e. signals reflect intentional labeling of external phenomena) – unless, inexplicably, monkeys *think* falling trees, trucks, and raptors constitute a singular class – yet the pattern is consistent with a motivation-structural model (Morton 1977, 1982) for signal evolution (i.e. use of *katrains* relates to a specifically high arousal state in callers).

The conclusion that *katrains* serve as a predator alarm still leaves the question of how signalers benefit. Of the typically proposed hypotheses, well summarized by Wheeler (2008), those relating to indirect fitness benefits include *kin selection*, *parental care*, and *mate protection* (i.e. signal increases likelihood of survival of the signaler's relatives – or specifically his offspring – or potential mates). The observation that resident males, occupying social groups teeming with potential mates, produce *katrains* whereas non-residents do not (Chapter 3) lends support to the latter. That males use *katrains* from the outset of their tenures, when their likelihood of having offspring present is low, suggests that benefits relating to parental care, though certainly nontrivial, may be of less primary importance. Hypotheses relating to *direct* fitness benefits of producing alarms, including the *selfish herd*, *predator confusion*, and *mobbing recruitment* hypotheses (reviewed in Wheeler 2008), find potential support in female blue monkeys' tendency to move, to move quickly, and to spend more time closer to the caller after hearing *katrains*; such responses might benefit the signaler if females' drawing closer or moving in ways that distract or repel the predator can reduce his own vulnerability. The observation that males sometimes actually attack eagles (Gautier-Hion & Tutin 1988; M. Cords pers. comm.),

thus making themselves *more* vulnerable, however, diminishes support for this explanation slightly. The *pursuit deterrence* hypothesis (i.e. predators that rely on surprise terminate their hunt if the prey is aware of their presence; Woodland et al. 1980) has been suggested for an alarm call of the closely related diana monkey (*C. diana*), with inferences drawn based on patterns of usage (Zuberbühler et al. 1997); though the considerable amplitude and audible distance of *katrains* (Brown 1989) may relate to this function, further research is required to determine if raptors actually do retreat.

With such overwhelming evidence of a role in predator avoidance, convention dictates that relating the *katrain's* function to anything other than its eliciting stimulus would be superfluous. That researchers often seem bound by convention, however, does not change the fact that natural selection most certainly is not. The *katrain's* rareness (one episode for roughly every 34 hours of observation) and its lack of association with any seasonal or demographic variables indicate that any benefits beyond predator avoidance are not likely major selection factors; secondary benefits, however, should not be discounted. Consistent with the mate defense hypothesis, non-resident males traveled farther distances after hearing *katrains*, and when they moved it was away from the caller 100% of the time (Fig 9). Resident males were equally likely to move toward or away from callers (Fig 10), a difference from non-residents that probably relates to residents' active defense against male intruders; future studies should examine whether residents' response is influenced by their position, and that of callers, relative to respective home ranges.

Kas

As described in Chapters 2 and 3, a strong relatedness between the *ka* and *katrain* is

demonstrated by the acoustic similarity (bordering on indistinguishability) of *kas* and the *katrain's* individual units as well as the calls' tendency to be used in the same contexts. The pattern of usage for *kas* was identical to that of *katrains*, with the same clear relationship to aerial predators and no other clear associations. *Kas* were rarely given alone and accompanied *katrains* with such consistency that examining the function of the *ka*, in isolation, was not possible. In the relatively few vocal episodes in which *kas* were not accompanied by *katrains*, contexts included tree falls and other loud disturbances, possibly suggesting that the *ka* reflects a similar yet slightly lower arousal state in callers. Future studies should examine whether contextual differences predict when callers will include *kas* with their *katrains*, and whether receiver response differs.

Ant

Though sample sizes precluded adequate examination of receiver response to hearing *ants*, indirect evidence of the call's function in predator avoidance is considerable and compelling. Of well-observed episodes that included *ants*, 74% were in predator contexts, and 84% of these involved terrestrial predators (Table 6). Threats that evoked *ants* were primarily dogs and snakes, a pattern consistent in both natural observations and simulations of these predators (Chapter 3, pp. 133-135). *Ants* were also produced in response to palm civets (*Nandinia binotata*) and baboons (*Papio anubis*), neither of which is known to prey on blue monkeys (and palm civets almost surely never could). Vocal episodes associated with these species were categorized as *heterospecific non-predator disturbances*, yet these associations may actually be consistent with (and thus provide even greater support for) a terrestrial predator alarm function. Baboons prey on

other primates (vervet monkey, *Chlorocebus pygerythrus*; Hausfater 1976) and thus may constitute a genuine threat to blue monkeys, and use of *ants* with civets may relate to a physical and phylogenetic affinity with other feliform carnivores (Kingdon 1988; Wozencraft 2005).

The specificity with which *ants* were used clearly identifies the call as a terrestrial predator alarm call, and suggests its potential to constitute a functionally referential call. Though occasionally occurring with other disturbances, including aerial threats and agonism with other males, such associations were uncommon and not significant. Observation that male blue monkey vocal signals apparently do not distinguish between terrestrial snakes and dogs appears counter to the example of vervet monkeys, a semi-terrestrial species classically shown to use distinct signals for snakes and leopards (Seyfarth et al. 1980). However, alarm signals that distinguish among potential threats have no evolutionary basis unless the *response* to these threats should differ (Marler 1977; Cheney & Seyfarth 1990; Macedonia & Evans 1993); for arboreal species (e.g. blue monkeys), the response "appropriate" to most terrestrial predators likely includes maintaining visual contact with the threat and mobbing (Srivastava 1991; Boesch & Boesch-Achermann 2000; Digweed et al. 2005; Gursky 2005), and is thus likely similar whether snake, dog, or leopard.

Future research should examine receiver response in relation to predator avoidance, and also investigate the potential for *ants* to dissuade predators from continuing a hunt. Anecdotal observations of males *anting* when no group mates were nearby to warn and, in other cases, a tendency to continue calling long after all group mates appeared fully aware of the position of the threat are consistent with the *perception advertisement* or

pursuit deterrent hypothesis (Sherman 1977; Woodland et al. 1980). Though this explanation may seem at odds with the popular view that snakes do not process airborne acoustic signals, research has demonstrated that snakes have a much greater ability to respond to auditory stimuli than commonly assumed (reviewed in Young 2003).

Beyond predator avoidance, the results of this study do not support other functional explanations for *ants*. Usage showed virtually no seasonal variation, occurring rarely yet consistently across months, and there was likewise no relationship with either the number of estrous females or infants in callers' groups. Though sample sizes were low, females appeared to spend less time around males after they *anted* (Table 14), contrary to any mate attraction function. The extreme rareness of the call (one episode of *ants* for roughly every 100 hours of observation per male), as well as its acoustic structure (Chapter 2, Table 6 and Fig. 4) are also inconsistent with repelling rival males; the low amplitude and higher frequencies of the *ant* relative to other call types renders it a poor candidate for long distance communication (Wiley & Richards 1982; Mitani & Stuht 1998).

Nasal Scream

The *nasal scream* was the least frequently observed call in the adult male repertoire, making systematic examination extremely difficult. Its consistency of usage, however, provides some insight to possible functions. During this study, as with previous observations of the call (M. Cords, pers. comm.), *nasal screams* were unambiguously associated with aggression between males, with the putative "loser" the animal that screamed (though see below). This observation is consistent with the functional explanation typically offered for *screams* (relatively high frequency, long, graded

vocalizations) in other species – that they are submissive signals that may avert or reduce aggression (e.g. rhesus macaques, *Macaca mulatta*; Maestipieri & Wallen 1997). As Owings and Morton (1998) suggest, higher frequency vocalizations are associated with smaller body size and infancy, and production of such signals by adults may function to deter attacks. Such loud, abrasive sounds may also serve to startle or distract an aggressor (Owren & Rendall 2001), providing opportunity for escape. In some primates, screams produced in aggressive contexts appear to recruit support for the screamer (e.g. rhesus macaques; Gouzoules et al. 1984; chimpanzees, *Pan troglodytes*; Slocombe & Zuberbühler 2007); such a function seems unlikely for blue monkey *nasal screams*, however, given that adult males are not known to form coalitions and females, being much smaller, are unlikely to fare well in a male fight.

During several decades of fieldwork in this population, there have been a few cases in which a male initiating attack, rather than the victim, was the animal that *nasal screamed* (M. Cords, pers. comm.). Such observations, though rare, are difficult to reconcile with an explanation as a submissive gesture. It is possible that, on a proximate level, this signal is associated with an intense state of arousal (i.e. fear) that may be experienced by either victims or attackers, yet is more often in the former. In chimpanzees (*Pan troglodytes*), for example, both aggressors and victims may scream during fights, though screaming by aggressors is less common and, notably, tends to be by low ranking or juvenile animals (Slocombe & Zuberbühler 2005).

Similarities to Congeners

The functional explanations identified in this study are similar to those for loud calls

across a variety of vertebrate taxa, indicating convergence on using distinct signals in response to a few primary social and ecological selection pressures. Not surprisingly, the patterns described for male blue monkeys calls resemble those in closely related species, particularly in regard to predator alarm signals. Arnold and Zuberbühler (2006) observed that adult male putty-nosed monkeys (*C. nictitans*) responded to the presence of eagles with short, low frequency *hacks* (resembling blue monkey *kas*), and used longer, more modulated *pyows* in response to leopards. In that study, the authors noted distinct *pyow* variants in the putty-nosed males' vocalizations, notably a "short *pyow*" quite similar to the blue monkey *ant* (see Fig. 2 in Arnold & Zuberbühler 2006), yet did not find a relationship between the variants and exposure to predator types. In another guenon, the Diana monkey (*C. diana*), adult males also use acoustically distinct calls associated with aerial and terrestrial predators (Zuberbühler et al. 1999; Zuberbühler 2000); here, both call types have multi-unit structures, but the "eagle call" is especially similar to blue monkey *katrains*. The multi-unit structure of *katrains* is shared in other *Cercopithecus* species, with Marler (1973) suggesting that the *katrains* of blue monkeys and redtail monkeys (*C. ascanius*) were "homologous"; anecdotal evidence during my study suggests redtail males use *katrains* also with aerial predators.

Though *booms* are shared by several other closely related guenons (see Chapter 2; Gautier 1988), a lack of systematic examination of *booms'* functions in other species makes it difficult to relate the findings for blue monkeys to a broader taxanomic context. The acoustic structure of guenon *booms* suggests potential function in distance communication (Wich & Nunn 2002), but further research is needed to determine if the affiliative function identified in blue monkey *booms* is shared in other species.

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Table 1a. Hypotheses and associated predictions examined for each call type in the male repertoire. For each hypothesis, evidence examined included patterns of call usage (seasonal and contextual), and responses by particular classes of receivers (Table 1b).

<table>
<tr><th rowspan="2">HYPOTHESIS</th><th rowspan="2">FUNCTIONAL DEFINITION</th><th colspan="4">PREDICTIONS (Usage)</th></tr>
<tr><th>Seasonal Variation</th><th>Demographic Variation</th><th colspan="2">Contextual Variation</th></tr>
<tr><td rowspan="4">Predator Avoidance</td><td rowspan="4">Signal evokes predator-avoidant behavior in kin or potential mates of signaler.</td><td rowspan="4">No prediction (seasonal and diel variation in predator presence and activity was unknown).</td><td rowspan="4">No prediction.</td><td rowspan="4">Signal is associated with the presence of predators.</td><td>1. With aerial predators.</td></tr>
<tr><td rowspan="3">2. With terrestrial predators.</td><td>2a. Dogs.</td></tr>
<tr><td>2b. Snakes (on ground).</td></tr>
<tr><td>2c. Humans.</td></tr>
<tr><td rowspan="2">Mate Defense</td><td>Signal evokes avoidance behavior in male competitors, including withdrawal from or lower likelihood of moving toward caller.</td><td>Call is produced more during mating season, June-September.</td><td>Call production rate correlates w/ number of estrous females in a group.</td><td colspan="2" rowspan="2">1. Signal is associated with the presence of other males (encounters and aggressive interactions).</td></tr>
<tr><td>Specifically infanticidal males.</td><td>No prediction.</td><td>Call production correlated w/ number of infants in group.</td></tr>
<tr><td>Mate Attraction</td><td>Signal evokes behavior in adult females that increases probability of caller's mating.</td><td>Call is produced more during mating season from June-October.</td><td>Call production rate is correlated with the number of estrous females in a group.</td><td colspan="2">No prediction.
(copulations may occur in any context and are frequently observed during aggressive inter-group encounters; non-disturbance, affiliative contexts, however, may be more conducive to mating).</td></tr>
<tr><td>Within-Group Cohesion</td><td>Signal facilitates behavior that increases proximity among group members and to caller.</td><td>No prediction.</td><td>No prediction.</td><td colspan="2">No prediction.
(benefits associated with intra-group connectivity are relevant to a variety of contexts, including inter-group encounters, predator events, presence of "intruder" males, and non-disturbance contexts.</td></tr>
</table>

Table 1b. Hypotheses and associated predictions examined for each call type in the male repertoire. Predictions here relate specifically to responses by different classes of receivers.

HYPOTHESIS	FUNCTIONAL DEFINITION	PREDICTIONS (Receiver Response)			
		Receiver Class			
		Resident Males	Non-Resident Males	Adult Females	
Predator Avoidance	(*see above*)	No prediction (predator-avoidant behavior by rival males unlikely to benefit signaler).	No prediction (predator-avoidant behavior by rival males unlikely to benefit signaler).	Exhibit predator-avoidant behavior after signal: - increase vigilance - increase proximity to others - increase "alarm" calls - collect infants (if applicable)	1. Aerial predator-avoidant behavior: - look up - move down - hide 2. Terrestrial predator-avoidant behavior: - look down - move up
Mate Defense	(*see above*)	Avoid signal origin after hearing. - increase or maintain distance - increase vigilance	Avoid signal origin after hearing. - increase or maintain distance - increase vigilance	No prediction.	
Mate Attraction	(*see above*)	No prediction.	No prediction.	Estrous females will increase proximity to caller (including approach and tolerate approach) after call.	
				Estrous females increase interaction with caller (e.g. proceptive display, mount, co-sit, groom) after call.	
Within-Group Cohesion	(*see above*)	No prediction.	No prediction.	- increase proximity to others - increase proximity to caller	

Table 2. Social groups observed during the study period, with the identity of resident males and group composition. Composition of groups not part of long-term study (bottom half of table; *) was unknown.

GROUP	**RESIDENT MALE(S)**	**INFLUX MALES**	**ADULT FEMALES** Mode (range)	**JUVENILES Both sexes** Mode (range)	**INFANTS Both sexes** Mode (range)
TWN	Quac	0	7 (7-8)	8 (7-9)	4 (3-5)
GSC	Perc	0	9 (8-10)	4 (4-7)	4 (3-6)
GSA	Sawa	0	11 (10-12)	7 (4-7)	8 (7-10)
GN	PH	3 (Aug-Sep, 2011)	15 (14-16)	23 (18-23)	12 (10-12)
TWS	Tip; Marv	4 (Sep-Oct, 2010) 3 (Aug-Sep, 2011)	17 (17-18)	27 (20-27)	8 (1-10)
GSB	Zomb; Fezi	*	*	*	*
ExF	Tige	*	*	*	*
F	Kent; Flipp; Idi	*	*	*	*
NE	Hoss; Axel	*	*	*	*
NW	NW-male	*	*	*	*
P	Mope; Xerox	*	*	*	*
TE	Pop	*	*	*	*

Table 3. Contextual variables used to score vocal episodes. *Disturbance* and *Non-Disturbance* are broad, exclusive categories that each includes several nested, non-exclusive contextual variables. Vocal episodes that included *Approach* and *Rejoin Group* occurred in both *Disturbance* and *Non-Disturbance* contexts, though primarily the latter.

CONTEXT					DESCRIPTION
DISTURBANCE	**Ecological**	Predator	Aerial	Raptor, Machine, or *Consistent*	Predator or loud machine (note: trucks, chainsaws, and airplanes evoke predator-consistent behavior in subjects and sympatric species; pers. obs.). *Consistent* indicates predators not observed but inferred from behavior by subjects and other species.
			Terrestrial	Dog, Human, Snake, Machine, or *Consistent*	
		Non-Predator		Tree Fall	Entire or large part of tree falling nearby with loud crash.
				Branch Fall	Branch falling nearby, quieter than tree fall.
				Meteorological	Thunder clap, lightening, earthquake.
				Heterospecific	Interaction with or attention directed to non-predator species (e.g. other primate, civet, bat).
	Social	Extra-Group	Other Male Nearby	Non-aggression	Behavior of caller and other male ranged from scanning and/or moving, to overt aggression (lunge, chase, grab).
				Aggression	
			Other Group Nearby	Non-aggression	Social group other than caller's nearby. Interaction between social groups was typically (though not always) aggressive.
				Aggression	
		Intra-Group	Aggression	With caller	Aggressive interaction (lunge, chase, grab, bite) between caller and member(s) of his group.
				Not with caller	Aggressive interaction among other members of caller's group.
	Unknown				Conspicuous increased arousal in group and/or caller (e.g. scan, move, vocalize); specific cause not identified.

(Table 3 continued on following page)

(Table 3 cont)

CONTEXT			DESCRIPTION
NON-DISTURBANCE	*Non-Disturbance* contexts all characterized by absence of any *Disturbance* variable. Caller and group rest or feed before and after call. No conspicuous indicators of arousal or anxiety in caller.	**Social Interaction**	Call precipitated by conspicuous, non-aggressive social interaction with caller (e.g. approach, copulation, proceptive behavior, grooming, monkey vocalizes while facing caller)
		Spontaneous	Call not precipitated by any conspicuous conspecific stimulus.
ALL CONTEXTS	**Approach**		Caller approaches / approached by conspecific, from ≥5m to ≤2m, and remains ≥5 secs with no aggression.
	Rejoin Group		Caller out of group ≥ 20 min moves toward group's center of mass and calls upon reaching group.

Table 4. Ethogram for 3-minute focal samples conducted after hearing a male vocalization (AV) and when no vocalization had occurred (NV). Subjects' activity was scored using all-occurrence sampling.

ACTIVITY		DEFINITION	
Look[1]		Subject unambiguously orients face and head in a direction different from prior to hearing vocalization.	Toward call origin
			Up (toward sky)
			Down (toward ground)
Flee[1]		General label for unambiguous escape behavior. Subject moved rapidly, in a directed manner, and typically toward cover.	Up
			Down
			Horizontal
Collect infant[1]		Subject moves directly toward and picks up, grasps, or sits ≤ 1m of infant. Only applicable if subject was ***not*** holding or co-sitting with infant at start of sample.	
Move		Subject moves ≥ 5m from start position (at one time, or in increments). Direction relative to call origin recorded:	Away (135º – 225º)
			Toward (≤45º; ≥315º)
			Neutral
Approach		Given or received; one party must be an adult male. Monkey moves from ≥5m to ≤2m of another, and remains ≥ 5 secs without aggression.	
Aggressive interaction		Subject gives or receives: - Submission: cower or flee from other monkey - Aggression: open-mouth or lunge threat, chase, grab, hit, or bite.	
Mating / proceptive [2]		- Mount (ejaculatory and non-ejaculatory not distinguished) - Give (female) or receive (male) proceptive behavior[1]: - present hindquarters - pucker: mouth open, lips compressed and protruded - headflag: shake head rapidly side to side	
Vocalize		Any vocal behavior other than cough or sneeze.	
Scan		While not feeding, move head side to side, with gaze directed elsewhere than substrate just in front. Accompanied by postural shift (e.g. sitting more upright), neck extension, and intense orientation.	
Displacement Behavior [3]	Scratch	Draw nails rapidly and repeatedly across skin.	
	Yawn	Head back, mouth fully open, canines fully displayed; if accompanied by indications of tiredness (e.g. closed eyes, reclining), distinguished "tired."	
	Shake	When not wet, subject moves body rapidly back and forth, as if ridding fur of water.	
	Auto-groom	Subject grooms self.	

[1] Recorded only if occurred during first minute of sample.

[2] Proceptive behavior is associated with initiating or escalating sexual interaction. In this species, the behaviors listed are strongly related to estrus and frequently precede copulation (Tsingalia & Rowell 1984; Cords 2002; Pazol 2003). These same behaviors, however, are sometimes (though rarely) observed in non-sexual contexts and may function occasionally as submissive gestures.

[3] Following Maestripieri et al. (1992), I considered these behaviors potential indicators of an animal's anxiety.

Table 5. Ethogram for 20-minute focal samples conducted after a male vocalization (AV) and when none had occurred (NV). Subjects' activity was scored using instantaneous and one-zero sampling at 1-minute intervals.

ACTIVITY		SAMPLING METHOD	DEFINITION
Feed / Forage		Instantaneous	Ingesting, handling, or localized movement directly related to food; includes searching immediate area and moving <2m between feeding sites.
Groom		Instantaneous	Subject gives or receives grooming: - move hands, fingers, or mouth through another's fur.
Move		Instantaneous	Walking, running, or leaping not associated with feeding.
Rest		Instantaneous	None of the above. May be sleeping, reclining, or sitting still.
Neighbors		Instantaneous	Number of conspecifics within 10m of focal subject.
Approach		One-Zero	(see Table 4)
Aggressive interaction		One-Zero	(see Table 4)
Mating / proceptive interaction		One-Zero	(see Table 4)
Vocalize		One-Zero	(see Table 4)
Scan		One-Zero	(see Table 4)
Displacement Behavior	Scratch	One-Zero	(see Table 4)
	Yawn	One-Zero	(see Table 4)
	Shake	One-Zero	(see Table 4)
	Auto-groom	One-Zero	(see Table 4)

Table 6. Hourly rate of usage for each call type (shown here as average monthly rate) across seasons for 5 resident males, observed for 721-939 hours each. Only *pyows* showed seasonal variation (Kruskal-Wallis rank sum test; tan shaded cell), being higher in Mating season (Nemenyi-Damico-Wolfe-Dunn *post hoc* test; yellow shaded cells).

CALL TYPE	SEASONAL CALL RATE Average ± SD (n=5)			Kruskal-Wallis chi-squared	df	*p*
	OFF (Apr-May; Nov-Dec)	BIRTH (Jan-Mar)	MATING (Jun-Oct)			
ANT	0.01 ± 0.013	0.01 ± 0.012	0.01 ± 0.014	0.1651	2	0.921
BOOM	0.386 ± 0.08	0.38 ± 0.0454	0.41 ± 0.073	2.9011	2	0.234
KA	0.015 ± 0.015	0.02 ± 0.012	0.02 ± 0.020	1.1023	2	0.576
KATRAIN	0.024 ± 0.018	0.03 ± 0.022	0.02 ± 0.019	0.5872	2	0.746
PYOW	0.318 ± 0.087	0.294 ± 0.079	0.36 ± 0.082	10.3638	2	**0.006**

Table 7. Results of Spearman's rank correlation tests, comparing hourly rate of usage for each call type to the number of estrous females in a group for 5 resident males. Only the positive correlation with *booms* was significant.

CALL TYPE	Rho	*p* (n=5)
ANT	-0.0229	0.8616
BOOM	0.6043	< 0.0001
KA	-0.0639	0.6271
KATRAIN	-0.0766	0.5606
PYOW	36679.43	0.8845

Table 8. Results of Spearman's rank correlation tests, comparing hourly rate of usage for each call type to the number of infants in a group for 5 resident males. No relationship was significant.

CALL TYPE	YOUNG INFANTS (<18 months)		ALL INFANTS (≤24 months)	
	Rho	p =	Rho	p =
ANT	0.1229	0.350	-0.0831	0.528
BOOM	0.0849	0.519	-0.0430	0.744
KA	0.1075	0.414	0.1927	0.140
KATRAIN	0.0017	0.989	0.2011	0.123
PYOW	-0.0975	0.459	-0.0645	0.625

Table 9. Records of naturally occurring vocal episodes, separated into *Disturbance* and *Non-Disturbance* contexts. Binomial tests (Bonferroni corrected alpha = 0.008) indicated *booms* occurred in *Disturbances* less than expected, whereas other call types occurred more in *Disturbances* than expected.

CALL TYPE	ALL VOCAL EPISODES	DISTURBANCE CONTEXTS	NON-DISTURBANCE CONTEXTS	p
ANT	76	75	1	<0.00001
BOOM	1716	850	866	<0.00001
KA	134	134	0	<0.00001
KATRAIN	199	199	0	<0.00001
PYOW	1481	1165	316	<0.00001

Table 10. Records of naturally occurring vocal episodes associated with predators. Binomial tests (Bonferroni corrected alpha = 0.008) indicated *kas* and *katrains* each occurred with aerial predators more and terrestrial predators less than expected. *Ants* occurred with terrestrial predators more than expected. *Pyows* occurred with terrestrial predators more and aerial predators less than expected. B*ooms* occurred with predators of any class less than expected.

CALL TYPE	ALL VOCAL EPISODES	ALL PREDATOR CONTEXTS	p =	AERIAL	p =	TERRESTRIAL	p =
ANT	76	56	<0.0001	7	1.00	47	<0.0001
BOOM	1716	73	<0.0001	13	<0.0001	60	<0.0001
KA	134	112	<0.0001	84	<0.0001	10	0.2641
KATRAIN	199	171	<0.0001	140	<0.0001	12	0.0297
PYOW	1481	368	0.0092	95	<0.0001	253	<0.0001

Table 11. Records of vocal episodes that occurred during encounters between adult males. Binomial tests (Bonferroni corrected alpha = 0.008) indicated *pyows* occurred with male agonism more than expected, whereas other call types occurred less than expected, though the relationship between *ants* and male agonism was not significant.

CALL TYPE	ALL VOCAL EPISODES	MALE AGONISM CONTEXTS	p =
ANT	76	12	0.3248
BOOM	1716	293	<0.0001
KA	134	7	<0.0001
KATRAIN	199	12	<0.0001
PYOW	1481	440	<0.0001

Table 12. Records of vocal episodes that occurred with *Approaches*. Binomial tests (Bonferroni corrected alpha = 0.008) indicated that *booms* occurred with *Approaches* more than expected by chance, whereas other call types occurred less than expected.

CALL TYPE	ALL VOCAL EPISODES	APPROACHES	p =
ANT	76	1	<0.0001
BOOM	1716	809	<0.0001
KA	134	0	<0.0001
KATRAIN	199	0	<0.0001
PYOW	1481	63	<0.0001

Table 13. Sample sizes for receiver responses to calls (AVs), separated by call type for different receiver sex and class and whether after naturally occurring or playback calls. For natural AVs, most subjects contributed multiple matched pairs; for playbacks, subjects were exposed to only one trial of each call type. For female receivers, social relationship to callers was either *familiar* (i.e. resident male of subject's group) or *stranger*. Female extended responses (20-min AVs) were examined only when caller was *familiar*; this sample size is first number under Natural AVs. Female immediate responses (3-min AVs) were examined for both *familiar* and *stranger* male calls; this sample size is the parenthetical number under Natural AVs and also all Playback AVs.

CALL TYPE	RECEIVER CLASS		NATURAL AVs	SUBJECTS	AVs PER SUBJECT median (range)	PLAYBACK AVs
BOOM	MALE	RESIDENT	150	8	28 (1-41)	5
		NON-RESIDENT	0	0	0	0
	FEMALE	ALL	663^{F} (42^{S})	61	9 (1-29)	21^{S}
		ESTROUS	207^{F} (15^{S})	21	11 (1-15)	9^{S}
PYOW	MALE	RESIDENT	465	9	55 (12-106)	7
		NON-RESIDENT	72	15	5 (1-13)	6
	FEMALE	ALL	603^{F} (34^{S})	61	10 (1-21)	29^{S}
		ESTROUS	156^{F} (14^{S})	16	8 (1-18)	10^{S}
KATRAIN	MALE	RESIDENT	57	7	9 (1-17)	6
		NON-RESIDENT	11	8	1 (1-2)	8
	FEMALE	ALL	121^{F} (32^{S})	41	3 (1-8)	31^{S}
		ESTROUS	28^{F} (12^{S})	12	2 (1-5)	14^{S}

^{F} denotes sample size for AVs in which caller was familiar (resident male of subject's group).
^{S} denotes sample size for AVs in which caller was stranger (resident male of another group).

Table 14. Comparison of males' time spent with neighbors and number of approaches after calling and after not calling. Separate analyses examined time spent with any neighbors, with successively larger groups of neighbors, and the number of approaches a male gave or received (Wilcoxon signed rank test, α =0.008). Values are given as proportions of 20-minute MNV and AV-Caller samples (i.e. number of *beeps* divided by 20) observed for each category; shaded cells indicate where AVs and MNVs were significantly different.

MATCHED PAIR SAMPLES	BOOM	PYOW	KATRAIN	ANT
Number of AV-MNV pairs	628	506	20	10
Number of Males	13	7	5	4
Pairs per male average (range)	48 (1-163)	72 (2-139)	4 (1-8)	3 (1-4)

ANY NEIGHBORS	**AV-CALLER mean ± SD**	0.77 ± 0.32	0.67 ± 0.36	0.70 ± 0.25	0.45 ± 0.38
	NV mean ± SD	0.59 ± 0.32	0.56 ± 0.14	0.65 ± 0.26	0.59 ± 0.16
	W	97928	72901.5	n/a	n/a
	p	2.2E-16	6.86E-05	n/a	n/a
1-2 NEIGHBORS	**AV-CALLER mean ± SD**	0.31 ± 0.23	0.31 ± 0.30	0.35 ± 0.39	0.25 ± 0.22
	NV mean ± SD	0.28 ± 0.15	0.29 ± 0.14	0.29 ± 0.19	0.29 ± 0.15
	W	77078	46795	n/a	n/a
	p	0.09576	0.2633	n/a	n/a
3-4 NEIGHBORS	**AV-CALLER mean ± SD**	0.25 ± 0.14	0.20 ± 0.26	0.24 ± 0.16	0.14 ± 0.16
	NV mean ± SD	0.17 ± 0.26	0.15 ± 0.07	0.19 ± 0.16	0.17 ± 0.08
	W	79825.5	47685	n/a	n/a
	p	1.16E-09	3.99E-06	n/a	n/a
>4 NEIGHBORS	**AV-CALLER mean ± SD**	0.17 ± 0.11	0.14 ± 0.26	0.09 ± 0.11	0.02 ± 0.03
	NV mean ± SD	0.12 ± 0.08	0.11 ± 0.08	0.15 ± 0.14	0.12 ± 0.08
	W	32400	18478	n/a	n/a
	p	0.0007	6.19E-05	n/a	n/a
APPROACH RECEIVED	**AV-CALLER mean ± SD**	0.04 ± 0.04	0.04 ± 0.02	0.02 ± 0.00	0.01 ± 0.01
	NV mean ± SD	0.03 ± 0.02	0.03 ± 0.02	0.03 ± 0.03	0.03 ± 0.02
	W	17332	1460.5	n/a	n/a
	p	0.00189	0.0141	n/a	n/a
APPROACH GIVEN	**AV-CALLER mean ± SD**	0.01 ± 0.01	0.01 ± 0.01	0.00 ± 0.00	0.01 ± 0.01
	NV mean ± SD	0.01 ± 0.01	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00
	W	3937	216	n/a	n/a
	P	0.0518	0.245	n/a	n/a

Table 15. Proportion of immediate responses (3-min focal samples) by female receivers in which subjects exhibited particular behaviors. Fisher's exact tests showed that some responses differed by call type (tan shading); post hoc tests (yellow shading) indicated differences related mostly to behavior being more likely after *katrains* than other calls.

	PROPORTION OF RESPONSES AFTER HEARING CALL							
	CALLER SAME GROUP (n= 228)				STRANGER (n=189)			
	BOOM	**PYOW**	**KATRAIN**	**p=**	**BOOM**	**PYOW**	**KATRAIN**	**p=**
Look *up*	0.02	0.02	0.05	0.068	0.01	0.02	0.04	0.468
Look *down*	0.01	0.01	0.03	0.395	0.02	0.02	0.03	0.794
Move *up*	0.03	0.03	0.04	0.623	0.03	0.02	0.05	0.382
Move *down*	0.01	0.01	0.08	<0.0001	0.04	0.01	0.07	0.005
Flee	0.00	0.00	0.05	<0.0001	0.00	0.00	0.06	<0.0001
Chirp	0.06	0.04	0.11	0.002	0.07	0.11	0.14	0.078
Growl	0.02	0.02	0.12	<0.0001	0.02	0.02	0.06	0.042
Scan	0.05	0.06	0.12	0.006	0.03	0.11	0.15	<0.0001
Proceptive	0.00	0.00	0.00	1.00	0.01	0.01	0.00	0.548
Collect infant	0.01	0.02	0.04	0.102	0.02	0.01	0.04	0.158

Table 16. Results of GLMs (separated by call type), examining association between subjects' activity and whether they heard a call by the resident male of their group. *Call Type*, presented here in the dependent position, is thus a binomial variable with levels *Heard* or *Not Heard*; shaded cells indicate where likelihoods of a behavior were significantly different in these levels. Note that estimates show relationships to *Not Heard* (i.e. negative values indicate a ***greater*** likelihood of occurring after hearing a call).

Call Type	Variable	Estimate	SE	z	p
Boom (n=663 AV-MNV pairs)	(intercept)	-0.244	0.274	-0.892	0.372
	Distance Moved	0.003	0.002	1.541	0.123
	Moved neutral to male	0.492	0.187	2.629	0.009
	Moved toward male	-0.940	0.238	-3.951	<0.001
	Time spent with male	-0.035	0.011	-3.132	0.002
	Approaches *from* male	-0.051	0.341	-0.149	0.882
	Approaches *given* male	0.333	0.331	1.006	0.314
	Proceptive interactions	-1.128	0.480	-2.351	0.019
	Time spent with any neighbors	0.013	0.014	0.964	0.335
	Time spent with 3-4 neighbors	-0.003	0.012	-0.232	0.817
	Time spent with >4 neighbors	-0.025	0.011	-2.293	0.022
	Vigilance scanning	0.002	0.014	0.178	0.859
	Chirps (alarm vocalization)	-0.036	0.066	-0.545	0.586
	Growls (alarm vocalization)	-0.097	0.137	-0.709	0.478
Pyow	(intercept)	0.766	0.277	2.767	0.006
	Distance Moved	-0.005	0.002	-3.152	0.002
	Moved neutral to male	-0.269	0.203	-1.325	0.185
	Moved toward male	-0.518	0.213	-2.434	0.015
	Time spent with male	-0.005	0.013	-0.402	0.688
	Approaches *from* male	0.244	0.401	0.607	0.544
	Approaches *given* male	-0.401	0.356	-1.126	0.260
	Proceptive interactions	-0.458	0.351	-1.304	0.192
	Time spent with any neighbors	0.005	1.019	0.005	0.996
	Time spent with 3-4 neighbors	-0.035	1.019	-0.034	0.973
	Time spent with >4 neighbors	-0.025	1.019	-0.025	0.980
	Vigilance scanning	-0.016	0.014	-1.146	0.252
	Chirps (alarm vocalization)	-0.122	0.076	-1.612	0.107
	Growls (alarm vocalization)	-0.101	0.157	-0.646	0.518
Katrain	(intercept)	0.724	1.136	0.637	0.524
	Distance Moved	0.009	0.009	0.990	0.322
	Moved neutral to male	1.044	0.767	1.361	0.174
	Moved toward male	1.064	0.750	1.418	0.156
	Time spent with male	-0.003	0.048	-0.059	0.953
	Approaches *from* male	16.000	788.215	0.020	0.984
	Approaches *given* male	-1.161	0.940	-1.236	0.216
	Proceptive interactions	0.390	0.962	0.406	0.685
	Time spent with any neighbors	0.053	0.053	0.998	0.318
	Time spent with 3-4 neighbors	-0.177	0.035	-5.035	<0.001
	Time spent with >4 neighbors	-0.151	0.037	-4.086	<0.001
	Vigilance scanning	-0.211	0.047	-4.504	<0.001
	Chirps (alarm vocalization)	0.258	0.218	1.186	0.236
	Growls (alarm vocalization)	0.462	0.591	0.783	0.434

Table 17. Results, summarized for each call type according to hypotheses and predictions in the Introduction. Cells marked with "+" indicate where results supported predictions, "0" where they did not, and "-" where results were opposite predictions. Cells with "±" indicate results were equivocal or not significant, yet tended towards support for the prediction. Darkened cells indicate observations were insufficient or indeterminate.

Hypothesis	Prediction		Boom	Pyow	Katrain	Ka	Ant
Predator Avoidance	Signal production associated with predators	Any	-	0	+	+	+
		Aerial	-	-	+	+	0
		Terrestrial	-	+	0	0	+
	Females increase general predator avoidant behavior	Scanning	0	0	+		
		Proximity to others	±	±	+		
		"Alarm" calls	0	0	+		
		Collect infant	0	0	0		
		Flee	0	0	+		
	… ***aerial*** predator-avoidant behavior	Look up	0	0	±		
		Move down	0	0	+		
	… ***terrestrial*** predator-avoidant behavior	Look down	0	0	0		
		Move up	0	0	0		
Mate Defense	Signal produced more during mating season		0	+	0	0	0
	Correlated with number of estrous females		+	0	0	0	0
	Correlated with number of infants (infanticide only)		0	0	0	0	0
	Associated with encounters with other males		-	+	-	-	0
	Males avoid signal origin	Residents	+	0	0		
		Non-residents		+	+		
Mate Attraction	Signal produced more during mating season		0	+	0	0	0
	Correlated with number of estrous females		+	0	0	0	0
	Females increase proximity to caller		+	+	0		
	Females increase interactions with caller (approaches, proceptive behavior, mounts)		+	0	0		
Within-Group Cohesion	Females increase proximity to group mates		±	±	+		
	Females increase proximity to caller		+	+	±		

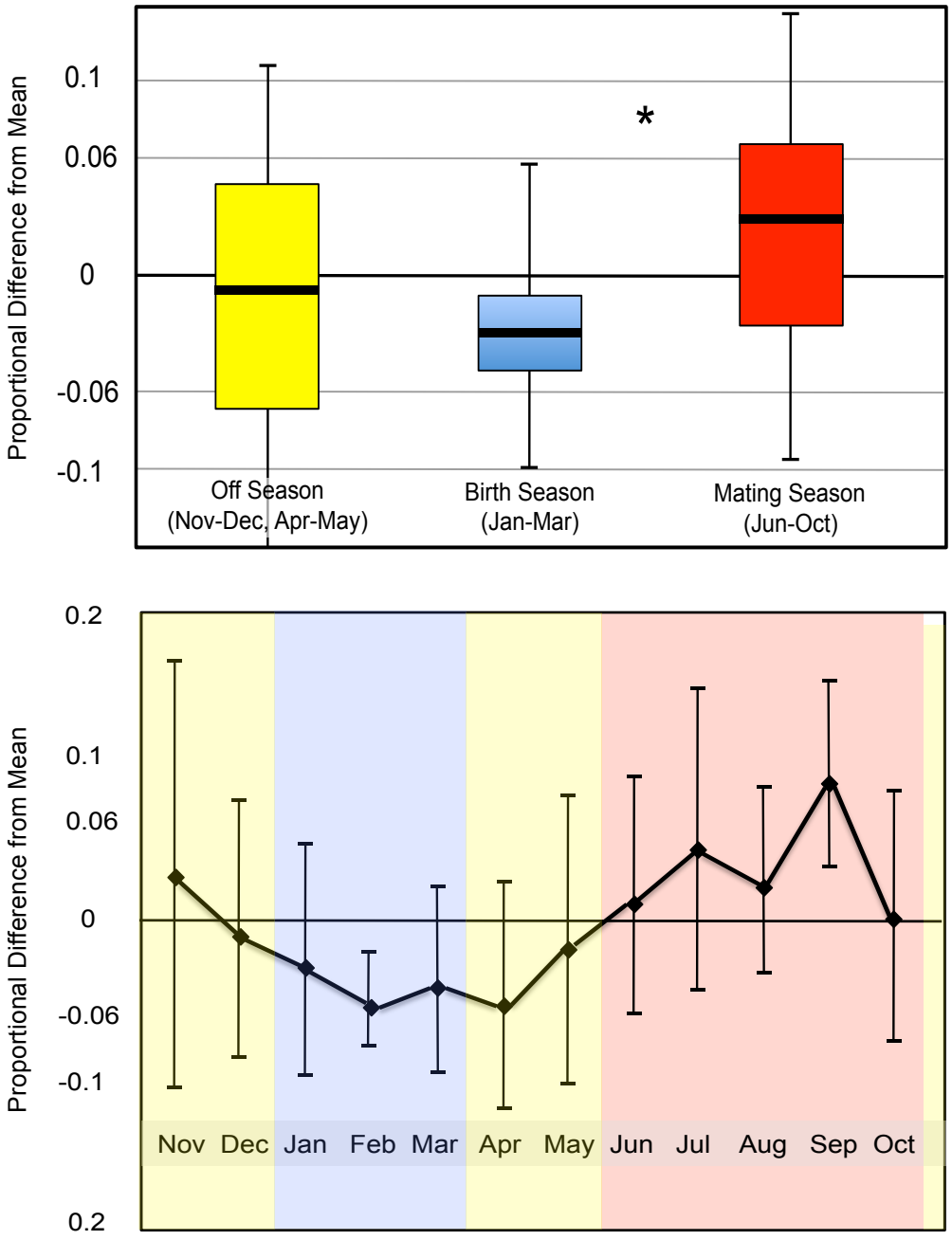

Figure 1. Rate of usage for *pyows* among seasons (Mating: red; Birth: blue; Off: yellow) for 5 males. *Pyows* were more frequent in Mating than Birth season (Kruskal-Wallis test; Nemenyi-Damico-Wolfe-Dunn *post hoc* test). Plots show variation in *pyow* rate across months (*bottom*; mean with one standard deviation) and condensed into seasons (*top*; boxes show median bound by IQR, whiskers show range); values are divergences from means.

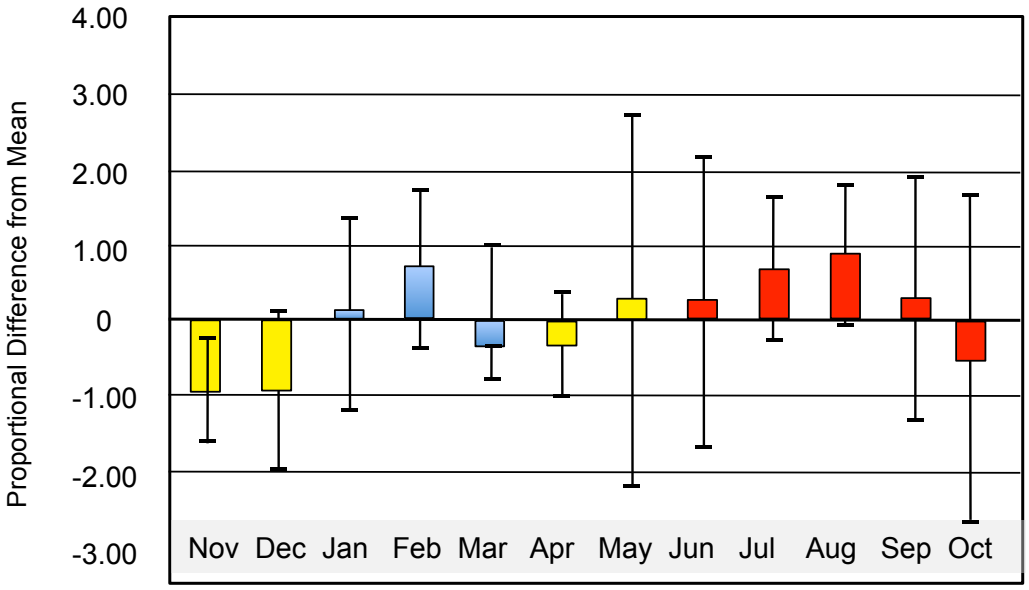

Figure 2. Number of unique females that copulated in a group each month (n= 5 groups). Values are average divergences from means; error bars show one standard deviation. Colors correspond with seasons (Mating: red; Birth: blue; Off: yellow).

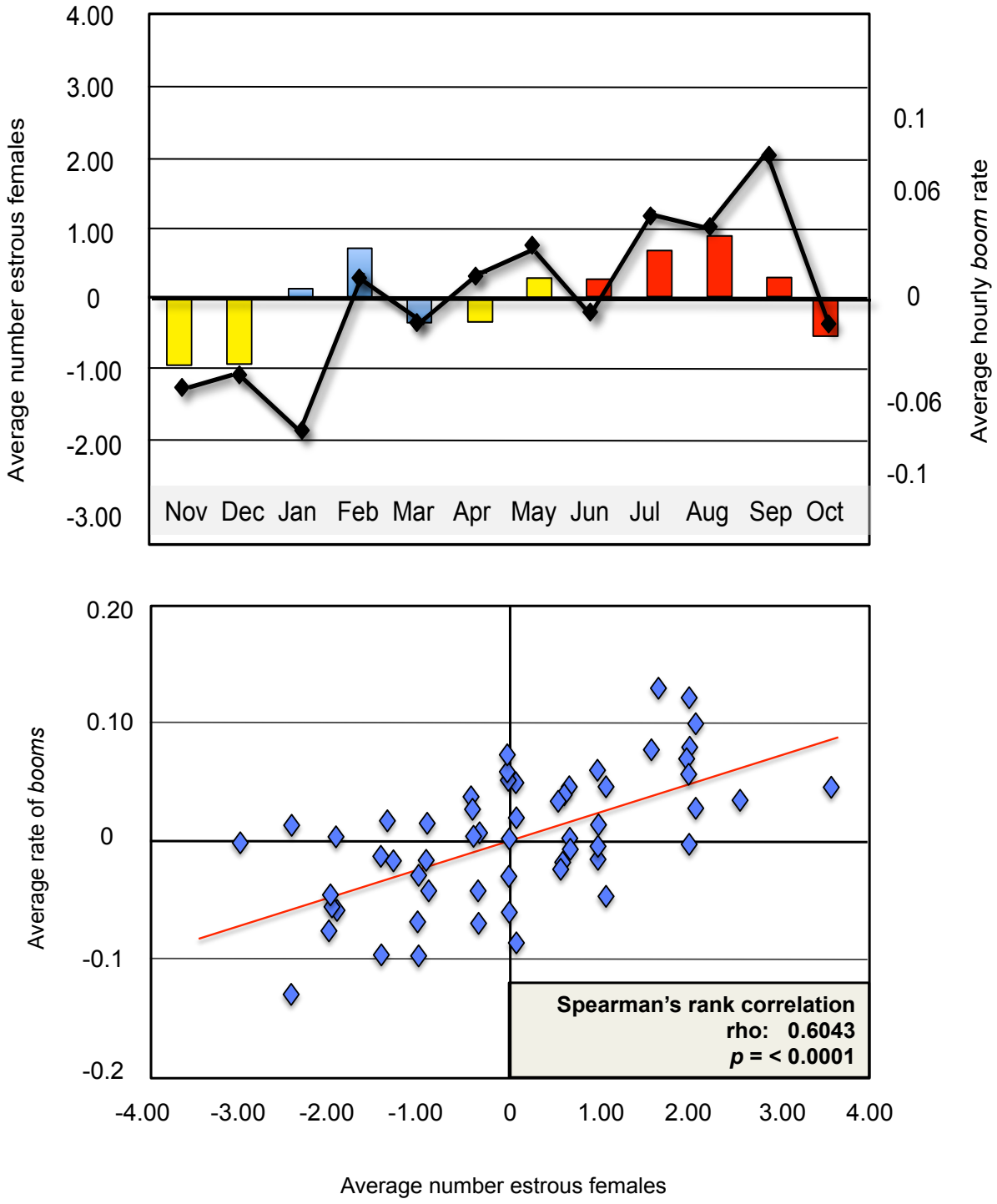

Figure 3. Relationship between rate of *booms* and number of estrous females in a male's group. Spearman's rank correlation test showed that males' (n=5) *boom* rate increased with the number of estrous females. Plots show monthly *boom* rates and number of estrous females in caller's group each month, centered around individual and group means, respectively. Top plot shows estrous females (bars) and *boom* rates (line) across months (error bars omitted). Colors indicate seasons (Mating: red; Birth: blue; Off: yellow).

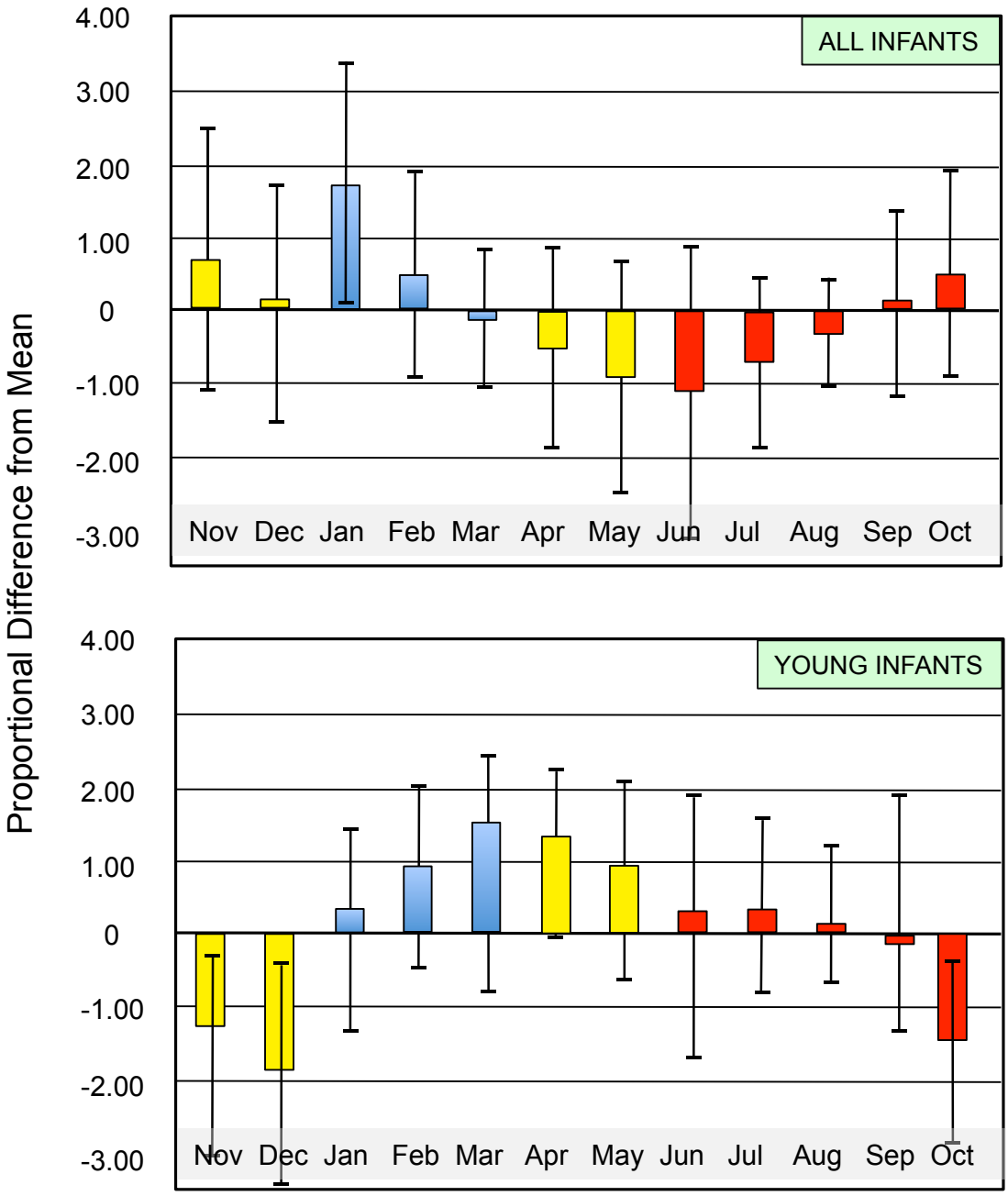

Figure 4. Number of infants ≤ 24 months (*top*) and <18 months (*bottom*) in groups (n= 5) each month. Values are average divergences from means; error bars show one standard deviation. Colors indicate seasons (Mating: red; Birth: blue; Off: yellow).

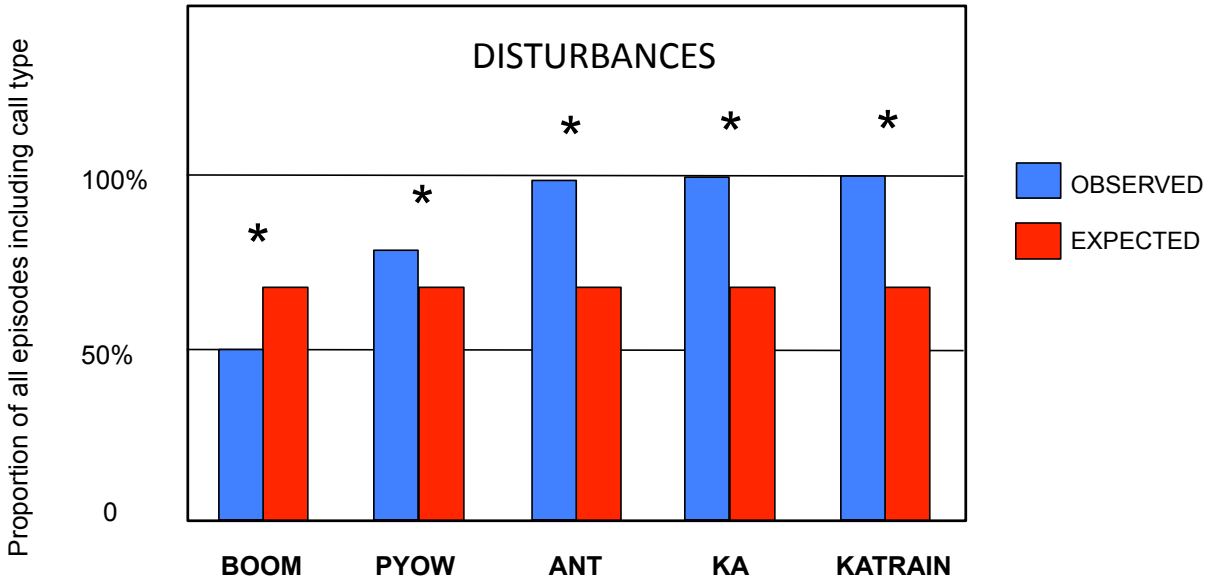

Figure 5. Proportion of each call types' occurrence in *Disturbance* contexts, compared to that expected under the null hypothesis that call type and context were independent (sample sizes in Table 9). *Booms* occurred equally in *Disturbances* and *Non-disturbances*, which was less in *Disturbances* than expected. Other calls occurred in *Disturbances* more than expected (binomial test, $p < 0.008$).

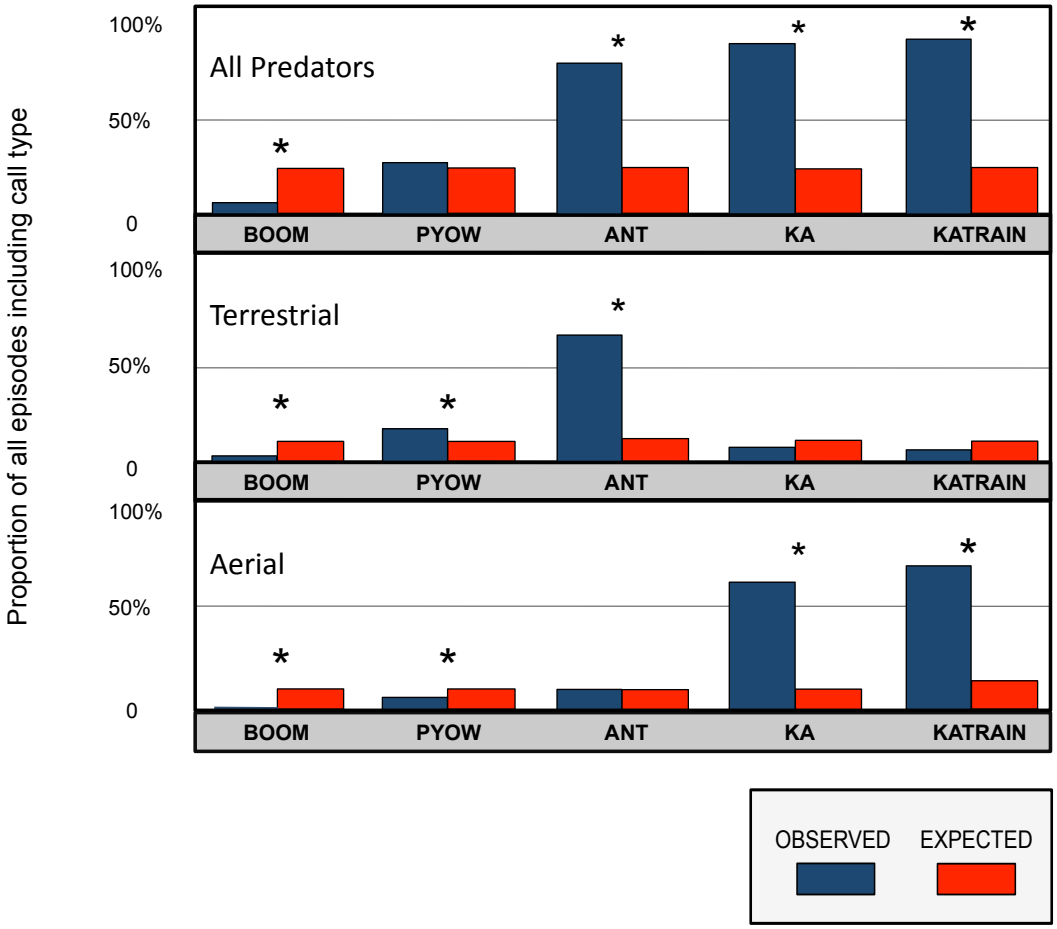

Figure 6. Records of naturally occurring vocal episodes associated with predators (sample sizes in Table 10). Binomial tests (Bonferroni corrected alpha = 0.008) indicated *kas* and *katrains* each occurred with aerial predators more and terrestrial predators less than expected under the null hypothesis that call type and context were independent. *Ants* occurred with terrestrial predators more than expected. *Pyows* occurred with terrestrial predators more and aerial predators less than expected. B*ooms* occurred with predators of any class less than expected.

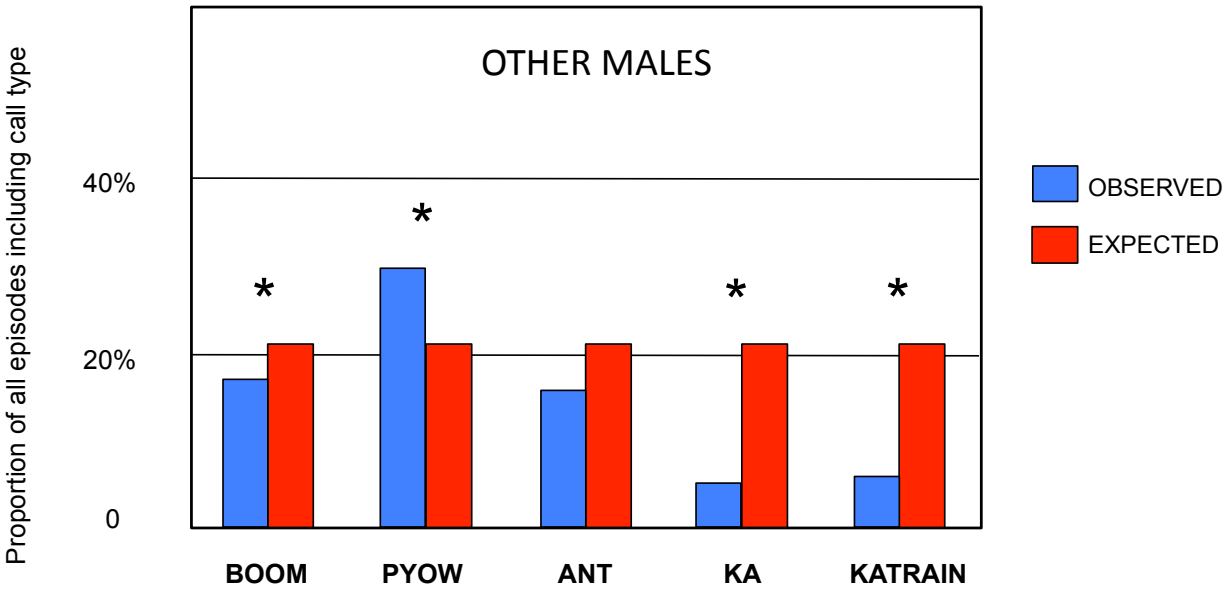

Figure 7. Vocal episodes that occurred during encounters between adult males (sample sizes in Table 11). Binomial tests (Bonferroni corrected alpha = 0.008) indicated *pyows* occurred with male agonism more than expected, whereas other call types occurred less, though the relationship between *ants* and male agonism was not significant.

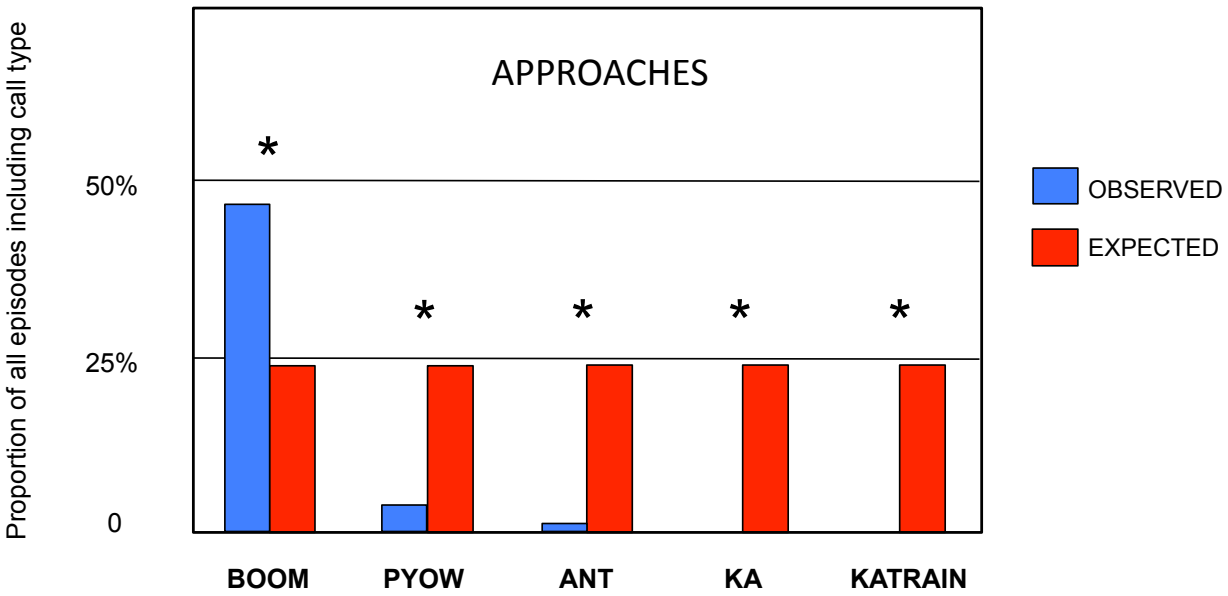

Figure 8. Vocal episodes that occurred with *Approaches* (sample sizes in Table 12). Binomial tests (Bonferroni corrected alpha = 0.008) indicated that *booms* occurred with *Approaches* more than expected, whereas other call types occurred less than expected.

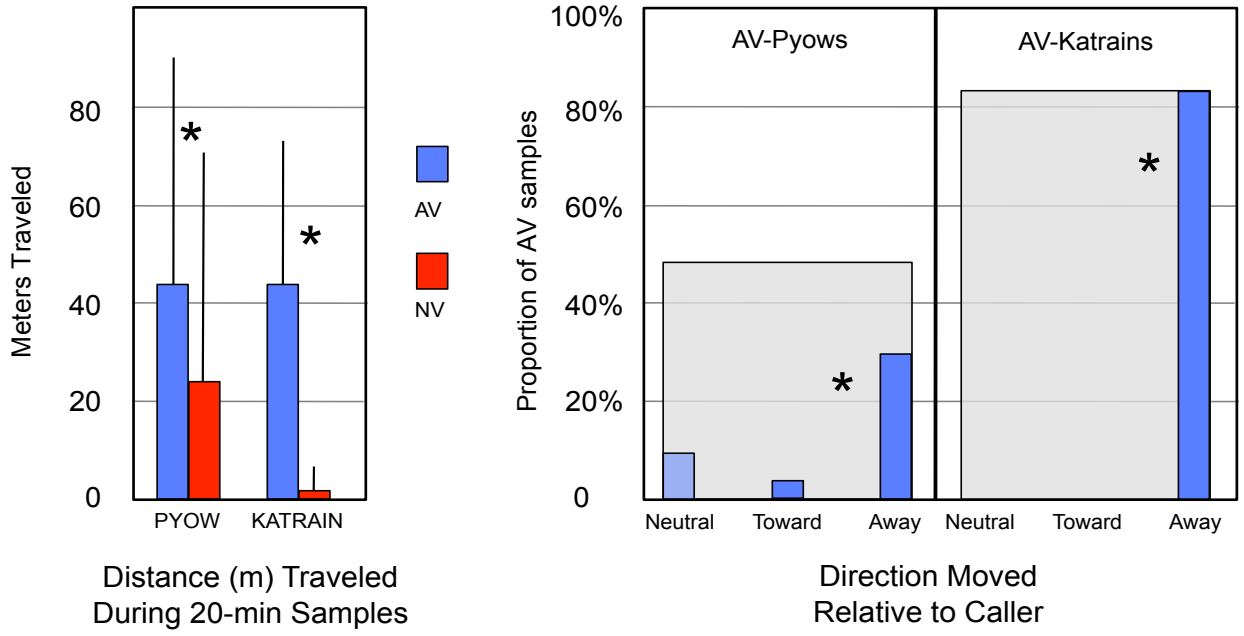

Figure 9. Non-resident males traveled farther (*left plot*) after hearing either *pyows* (n=15 males, 72 AV-MNV pairs) or *katrains* (n=8 males, 11 AV-MNV pairs) than after no call (Wilcoxon signed rank test). When subjects moved >25m after a call (*right plot*; gray outlines) they were more likely to move away from the caller than toward (binomial test).

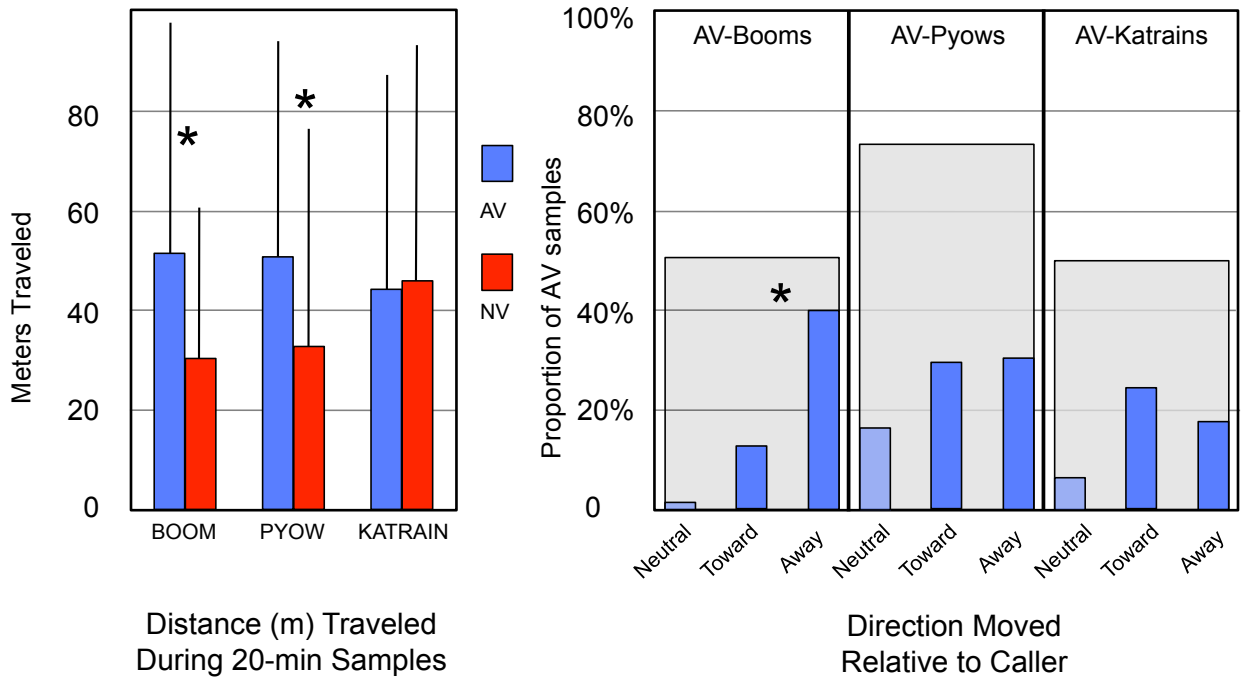

Figure 10. Resident males traveled farther (*left plot*) after hearing either *booms* (n=8 males, 150 AV-MNV pairs) or *pyows* (n=9 males, 465 AV-MNV pairs) than after no call (Wilcoxon signed rank test). When subjects moved >25m after a call (*right plot*; gray outlines), they were more likely to move away from the caller than toward if the call was a *boom* (binomial test).

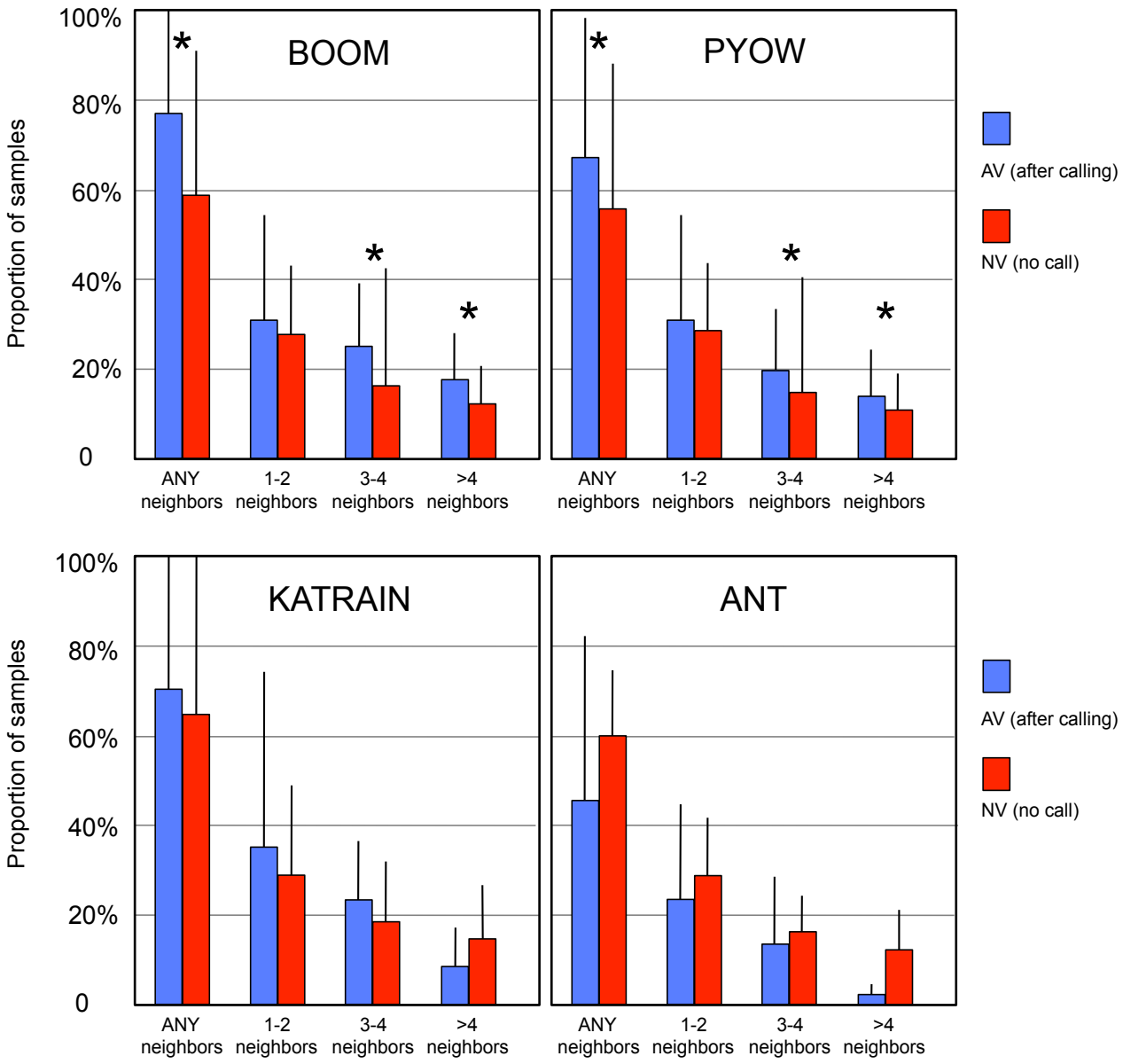

Figure 11. Time spent with neighbors after calling compared to after not calling (matched pair analyses; sample sizes in Table 14). Values (means; error bars show one standard deviation) are shown as the percentage of each focal sample (i.e. *beeps* out of 20) that males spent with any neighbors and with different numbers of neighbors. Wilcoxon signed rank tests (α =0.008) showed that males spent more time with neighbors and with greater numbers of neighbors after producing *booms* and *pyows* than after not calling. No analyses were conducted for *ants* and *katrains* due to small sample sizes.

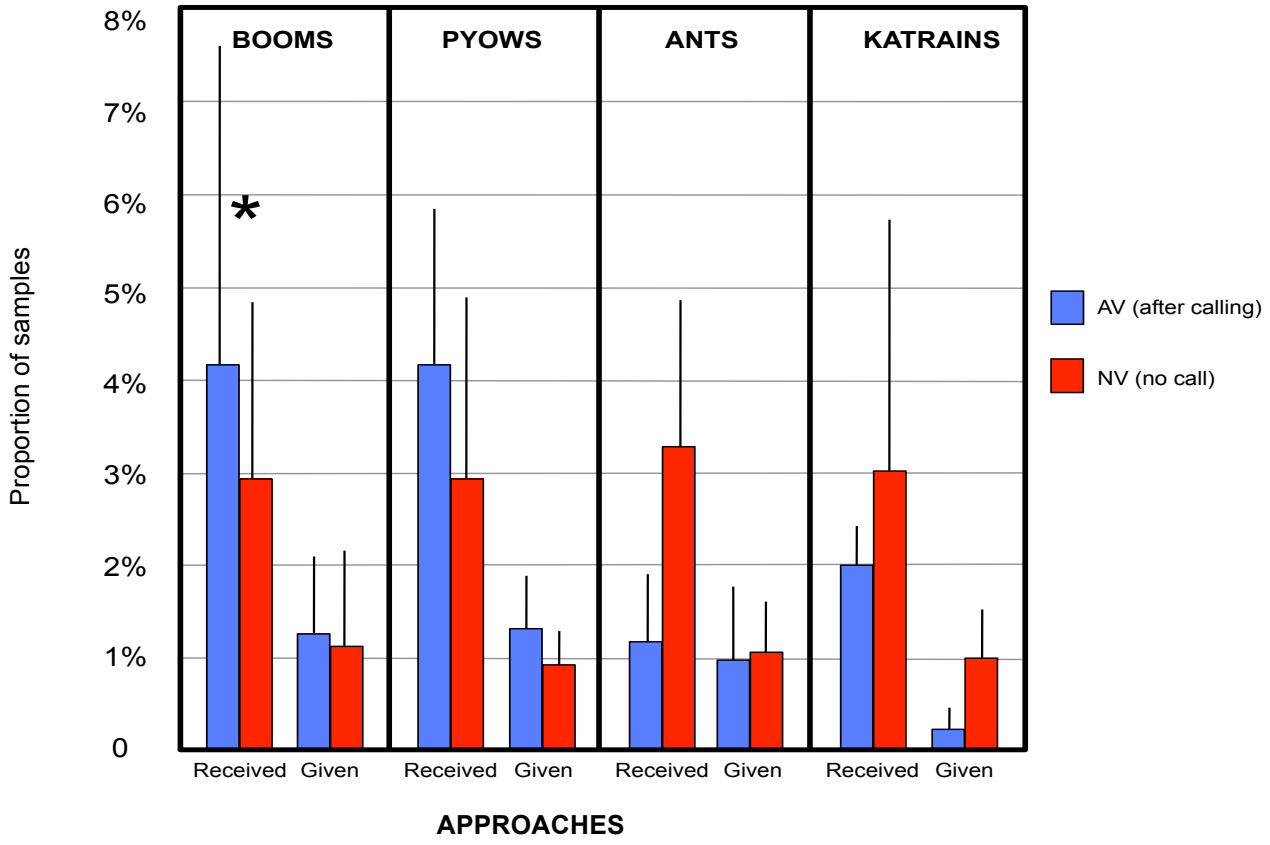

Figure 12. Proportion of samples in which approaches were given or received by a male after calling compared to after not calling (matched pair analyses; samples sizes in Table 14). Values (means; error bars show one standard deviation) are shown as proportion of *beeps* in focal samples (i.e. *beeps* out of 20) that males approached or were approached by conspecifics. Wilcoxon signed rank tests (α =0.008) showed that males received more approaches after producing *booms* than after not calling; the greater number of approaches received after *pyows* was not significant (p=0.014). No analyses were conducted for *ants* and *katrains* due to small sample sizes.

CHAPTER 5

The vocal repertoire of adult male blue monkeys (*Cercopithecus mitis stuhlmanni*): an integrated inquiry.

We have to remember that what we observe is not nature in itself, but nature exposed to our method of questioning. - Werner Heisenberg (1962)

Conventionally, researchers rely on a deconstructionist approach to animal communication, analyzing component parts such as type of signal, acoustic variation, content, or adaptive functions in separate investigations. This approach facilitates focused investigations and has yielded significant progress in understanding of the usage and evolution of signals. Like the many bones of a bird's wing, however, the individual elements of animals' communication systems collectively comprise something altogether different from what their constituent parts could possibly describe.

At the outset of this dissertation, I posed a "simple" question – what selection factors drive divergence among signals? The complex, multidimensional nature of selection, unfortunately, rarely lends itself to simple answers. Taken in their entirety, however, the investigations detailed in the preceding chapters provide opportunity for an integrative approach to understanding the vocal repertoire of male blue monkeys and the evolution of signaling systems. The following sections *1*) summarize the primary results of this study; *2*) examine functional explanations for call types in relation to the identified elements of signal content; *3*) explore an evolutionary hypothesis for signal divergence in this repertoire based on patterns of acoustic distinctness among call types and their described content and function; and *4*) propose avenues of future research.

SUMMARY REVIEW OF RESULTS

Chapter 2: Acoustic Structure The vocal repertoire of adult male blue monkeys (*Cercopithcus mitis stuhlmanni*) comprises six acoustically distinct call types: *boom*, *pyow*, *ant*, *ka*, *katrain*, and *nasal scream*. Each call type is distinguishable by ear, visual inspection of spectrograms, and by using acoustic features in discriminant function analysis. Differing degrees of acoustic similarity among the call types indicate three primary acoustic structures of the repertoire – an extremely low frequency, non-harmonic *boom*, a highly variable, harsh *nasal scream*, and a downward sloping 2- to 3-frequency-band structure that characterizes the *pyow*, *ant*, *ka*, and individual units of the *katrain*.

Cluster analyses reveal that the *pyow* and *ant* are closely related, with some recordings (particularly from vocal episodes in which extended bouts of *pyows* switch to *ants*) giving the appearance of a graded, transitional form between the two calls and suggesting the *ant* is derived from progressively shortened, harsher *pyows*. Analyses also demonstrated that, acoustically, individual units of the *katrain* are practically identical to *kas* given singly; the multi-unit structure of the *katrain*, unique within the male repertoire, is basically a series of rapidly repeated *kas* with a short, guttural *urr* sound connecting them. The acoustic structure of the *boom*, lacking harmonics and with a center frequency nearly ten times lower than other calls, reflects its heavy reliance on the males' supralaryngeal air sac (Gautier 1971; Fitch & Hauser 1995) and suggests *boom* production is fundamentally distinct from all other call types.

Chapter 3: Signal Content Clear relationships between signal features and signaler attributes indicate where some calls in the male vocal repertoire are reliable

indicators of various intrinsic and extrinsic attributes. With the exception of the extremely rare *nasal scream*, each call type includes **social status** as signal content; males holding resident or influx status (i.e. occupying a social group) used each of the six call types of the repertoire, whereas non-resident males appear to use only the *nasal scream*. **Individual identity** is content for the *boom*, *pyow*, and *katrain* (i.e. samples of calls were correctly assigned to callers based on acoustic features); sample size was inadequate to test individual distinctiveness for other call types, though similarities in structure and mode of production suggest they also may indicate identity. The observation that *pyows* are reliable indicators of a caller's **body size** is tempered, somewhat, by the concurrent observation that males measured in this study differ very little in skeletal length; other variables associated with male resource holding potential, such as energetic condition, muscle mass, or testosterone, might be of greater biological importance. Though further study is required, it seems likely that intrinsic content elements – status, identity, and size (and perhaps others such as condition, age, and tenure) – tend to be common to calls across the repertoire, whereas extrinsic attributes (below) are more call-specific.

Four call types – the *ant*, *ka*, *katrain*, and *nasal scream* – were reliable indicators of particular external variables whereas *booms* and *pyows* were not. The extreme consistency with which *nasal screams* were used during aggressive interactions with other adult males makes them reliable indicators of the **presence of other males**; this content element is potentially relevant to female receivers, but the response *by the other male* is undoubtedly of greatest relevance to callers and selection on *nasal screams* therefore likely relates to other, currently unidentified signal content. Content of *ants*

included the caller's attention to **terrestrial threats**, occurring primarily with snakes on the ground and dogs, though sometimes also in response to baboons, civets, and motorcycles. *Kas* and *katrains* each included the presence of **aerial threats** as content, produced consistently in response to raptors and the occasional low flying aircraft.

Chapter 4: Signal Function Most of the vocal signals used by adult male blue monkeys appear to serve multiple functions, evoking distinct responses from females and other adult males. The two most frequently used call types, *booms* and *pyows*, function as somewhat general advertisement signals, whereas *ants*, *kas*, and *katrains* fit classic models of predator specific alarm calls. The function(s) of the *nasal scream* could not be adequately examined due to its extreme rareness, yet a role in male-male aggression is clear; further research is necessary to determine how the *nasal scream* may function as a submissive, aggressive, or aggression avoidance gesture.

Both *kas* and *katrains* relate to aerial predator avoidance, with evidence that *katrains* are functionally referential (*sensu* Marler et al. 1992). These calls are produced nearly exclusively with aerial predators, and female receivers typically respond by moving down, increasing vigilance, and increasing proximity to neighbors. *Katrains* (and perhaps also *kas*, though data were not available) also function in repelling rival males, with non-resident males typically moving away from callers. Given the relative rareness of the *katrain* and its clear association with aerial predators as stimulus, repelling rivals is perhaps best considered a secondary, though nonetheless important selection factor.

The rareness and relatively short audible distance of *ants* limited examination, yet the call's consistent use with terrestrial threats – predominantly with snakes on the ground

but also dogs, and baboons – clearly indicates a function relating to terrestrial predators. Future research should examine receiver response (including that of predators) and the potential for the *ant* to constitute a functionally referential call.

Booms and *pyows* are the most frequently used calls of the male repertoire, and each appears to serve multiple functions relating to mate defense, mate attraction, and group cohesion. The *pyow* is best summarized as a general alert/advertisement signal, with primary benefits relating to repelling rival males and group cohesion. *Pyows* were associated with a wide variety of stimuli and contexts and, though sometimes produced "spontaneously" in peaceful contexts or during group movement, were typically evoked by some type of disturbance, including the presence of other males, predators, and within-group aggression. After hearing *pyows*, females in the caller's group typically oriented and moved toward the caller and increased proximity to group mates, whereas non-resident males typically moved away from callers. The *boom* was similarly observed in practically every possible context, yet functionally is clearly associated with affiliative interactions. The *boom* was the only call type used more often in non-disturbance contexts and that resulted in an increase in affiliative interactions between the caller and other monkeys, with strong evidence that it constitutes a signal of benign intent (*sensu* Silk 2002; facilitates affiliative interactions by "advertising" a lack of aggression). A function relating to mate attraction for the *boom* is indicated by the call's association with the presence of estrous females and the observed increase in proceptive displays and copulations after calls. Evidence that *booms* also repel rival males indicates a dual function in mate attraction and defense.

RECEIVER RESPONSE AND SIGNAL CONTENT

The stereotyped signals of a species repertoire reflect selection that balances fitness priorities of both signalers and receivers (Krebs & Dawkins 1984; Krebs & Davies 1993). In short, signalers produce a particular signal because, on balance, they benefit from receivers' responses. Receivers, in turn, respond to a signal in a particular way because, on balance, they benefit by doing so. As discussed in Chapters 1 and 3, for selection to favor receivers' responding to a signal in a consistent manner, signal content must relate in some way to receivers' fitness.

In this section, I examine functional explanations offered for male signals (Chapter 4) in relation to the elements of signal content identified in Chapter 3. For organizational purposes, I address receiver responses relating to different functional hypotheses separately. Sample sizes for responses to the *ant*, *ka*, and *nasal scream* were not adequate for this particular examination; further study of these signals is eagerly anticipated.

All Hypotheses Though not explicitly addressed in Chapter 3, it is important to consider that vocalizations, first and perhaps foremost, draw receivers' attention to the caller, making the caller's **presence** (and presumably species and sex; Owings & Morton 1998) an element of content. Furthermore, male blue monkey calls are loud and abrupt, and thus structurally ideal for triggering an acoustic startle reflex in receivers (Eaton 1984; Owren & Rendall 2001). Though perhaps easy to overlook for its ubiquity, *presence* as signal content is hardly inconsequential. The fact that male signals announce the caller's presence, and in a manner likely to impel receivers to orient and increase attention (Herzog & Hopf 1984; Owren & Rendall 2001), is necessary and in some cases

may be sufficient to explain some receiver responses, regardless of other content elements. For example, in cases where an animal is likely to respond predictably to another stimulus (e.g. seeing a predator, food source, or familiar adult male), a simple "alerting" signal may trigger a secondary response (e.g. hide, approach) that functions as the primary adaptive benefit of the signal.

Predator Avoidance Upon hearing *katrains*, the most conspicuous receiver response is the tendency of females to flee and move downward; receivers also appeared twice as likely to look up after *katrains* than other calls, though this increase was not significant ($p=0.068$). In terms of selection, this behavioral pattern is best explained by the fact that more than 85% of all *katrains* were associated with predators, and primarily aerial threats. Because selection is a probabilistic process, even if *katrains* sometimes are evoked by other stimuli (e.g. falling trees), the high consistency of association with aerial predators is sufficient to favor a consistent raptor-appropriate response.

Other responses to *katrains* by female receivers – increased vigilance and moving closer to other group mates – could relate to a general alerting function (above), though they are also consistent with anti-predator behavior (Pitcher & Parrish 1993). This tendency for group members to spend more time with neighbors after *katrains* illustrates how predator avoidance may be both cause and consequence of maintaining group cohesion. That females in a caller's group moved toward the caller after *katrains* also relates to predator avoidance, yet is likely mediated by the call's inclusion of identity as content; given the importance of individualized relationships in primates' social lives (de Waal & Tyack 2003) and the potential threat of "stranger" males to blue monkey infants

(Cords & Fuller 2010), females are likely to discriminate among callers. Caller identity may also relate to female anti-predator response if callers have previously demonstrated an ability to defend group members against potential threats (i.e. are "reliable;" Blumstein et al. 2004); the apparent urgency observed in receiver responses even to *katrains* by unfamiliar males, however, indicates the association with predators is the primary explanatory agent of females' response to *katrains*.

Mate Defense The response by adult males, and non-resident receivers in particular, appears consistent across call types – male receivers tend to move away from male callers. Intense aggression is common when adult male blue monkeys encounter one another (Tsingalia & Rowell 1984; pers. obs.), and the fact that all call types reliably indicate callers' age-sex class thus partly explains this response. That the calls reliably indicate males' status (i.e. only resident males call) also likely relates to non-residents' tendency to retreat. In blue monkeys, as in territorial species, resident status is indicative of a willingness to aggressively defend females or other resources, and non-residents should therefore respond to any call by a resident male as a potential threat. Furthermore, if non-resident receivers remember past encounters with *particular* individuals, identity as signal content could supplement a repelling function by associating the signal with aggressive characteristics of the caller (Rubenstein & Hack 1992).

Though blue monkey loud calls function in repelling non-residents, among residents they appear to function, more subtly, as a mechanism for mutual avoidance (Waser 1975). Such a function could relate to calls' being indicators of both resident status and individual identity, though the degree to which blue monkey males "respect" the spatial

boundaries of neighboring residents is unclear. It was noted during field observations (though not directly examined for this study) that resident male receivers often appeared to ignore calls if the caller was in the "correct" home range. This pattern is consistent with the "dear enemy hypothesis" in which territory holders discriminate between strangers (i.e. potential invaders) and familiar neighbors (i.e. "dear enemies") based on acoustic features of calls (Wiley 2005).

Unlike *booms* or *pyows*, *katrains* were unambiguously associated with aerial predators, suggesting that predators as content might also explain the response by male receivers. Avoiding predators and avoiding rival males might look remarkably similar and could equally fulfill the mate defense function, making it difficult to assess the *mechanism* by which the function is achieved. At least two observations, however, suggest males' retreating is better explained by signal content reflecting characteristics of the caller rather than the presence of raptors. Whereas female response to *katrains* (natural or playbacks) was typically conspicuous and immediate, male receivers never dropped down or hid and when moving away, did so gradually and often at the same height (Chap 4, p. 201). Secondly, because raptors can easily cover hundreds of meters quickly, moving away from a caller (even assuming the predator is near the caller) would have little anti-predator value, and might in fact attract the predator's attention.

That signal content includes body size, at least for *pyows*, could relate to males' retreating, as it does for several other species (e.g. frogs, Gerhardt & Huber 2002; deer, Reby et al. 2005). Among the resident males examined in this study, however, skeletal size differed very little (Chap 3) and, though some non-residents might be smaller than some residents, other factors associated with fighting ability are likely more important.

Future studies should examine whether signal content includes caller attributes such as energetic condition, testosterone, and likelihood of escalating aggression.

Mate Attraction In some species, the direct approach of a male by an estrous female typically results in mating (e.g. deer, Clutton-Brock et al. 1982; frogs, Arak 1983). In primates and other taxa in which the sexes interact more frequently, however, proximity between males and females can sometimes relate to non-reproductive functions (e.g. grooming, infant care). In outlining criteria for inferring sexual selection on primate signals, Snowdon (2004) therefore included that the expression of preference for a signaler, subsequent to the signal, must relate specifically to a reproductive context. In other words, simply increasing proximity to a male after he calls should not constitute evidence of mate attraction unless mating is involved. Under this criterion, because mating behavior was not commonly observed immediately following *pyows* and *katrains*, the tendency for females to move toward callers after these calls is better explained by other functions (i.e. group cohesion, predator avoidance). However, in species in which mating decisions likely are based on a wide variety of factors and reflect the cumulative influence of numerous interactions, it can be difficult to assess the relationship between producing a signal and mating behavior in any sort of direct fashion.

It is reasonable to state that any behavior that increases proximity between males and females relates to the actor's *potential* for mating. Therefore, while intersexual selection should probably be considered of secondary importance for *pyows* and *katrains*, their ability to facilitate interactions between a caller and females does relate at least indirectly to mating opportunities. The inclusion of identity and social status likely relates to female

phonotaxis following these calls (above). Female preference for males that call may also relate to calls' function in mate defense; if calls (or particular features of calls) successfully repel rival males, staying close to callers may provide females protection against aggression by other males (Borgia 1979) and mating with "effective" callers may increase the fitness potential of offspring (Andersson 1994).

Evidence of the *boom's* function in mate attraction is much more direct than for other calls, including an increase in affiliative interactions (including proceptive displays and mounts) after the call and a clear association between usage of *booms* and the number of estrous females in a group. That females exhibit mating preference based on males' vocal signals is well established in birds (Catchpole & Slater 1995) and anurans (Gerhardt & Huber 2002), with convincing but limited evidence in some mammals (Clutton-Brock & McAuliffe 2009). What specific benefits to females these signals relate to, however, remains less well understood. Most studies suggest that signals functioning in mate attraction are effective because they advertise male "quality," either in a general, undefined sense, or in relation to specific attributes such as body size or genetic characteristics. *Booms* may indeed advertise male attributes such as energetic condition or genetic superiority, but observations suggest their role as signals of benign intent best explains their function in mating. *Booms* are frequently evoked by females' approaching and producing *long grunts*, thus reducing the importance of advertising attributes such as identity or body size (i.e. the receiver most likely to participate in affiliative interactions after *booms* can see these for herself). *Booms* thus appear to differ considerably from "advertisement" mating signals such as bird song, deer roars, frog croaks, or elephant rumbles that attract potential mates from considerable distances. Rather than

physiological attributes that determine a male's "quality", female response to *booms* may relate more to the caller's subsequent behavior. A female's decision to approach a male proceptively likely relates to her state of estrus and numerous factors about the male (e.g. status, condition, age). When approaching a male, however, females are at risk of aggression, and thus hesitating until some signal of benign intent has been provided would be advantageous. Future studies should examine whether males' use of *booms* shows a pattern of preference for particular females or females in particular classes (e.g. ovulating, multiparous, high ranking).

Group Cohesion To achieve the numerous benefits of group living (Krause & Ruxton 2002), animals must maintain some degree of proximity to one another. In many group living species, and especially those living in visually obstructed environments or in which individuals are highly dispersed, vocal signals play a key role in maintaining connection among group members (da Cunha & Byrne 2009). Signals that function to facilitate or maintain group cohesion generally appear to do so by coordinating travel, allowing animals to monitor the whereabouts of group members (e.g. "contact" calls), or by attracting receivers to a caller or shared resource (McComb & Reby 2005).

To varying degrees, each of the three calls examined (and potentially *ants* and *kas* as well) increases proximity among group members and impels female receivers to move closer to callers. The most parsimonious explanation for this response relates to calls' function as an alert signal and their content of *presence* (above) – if we assume that the attention spans of monkeys, like many species (and some graduate students), are limited and easily expended in foraging, resting, or interacting with preferred social partners, the

loud, abrupt calls of males could suffice to re-engage attention to monitoring group mates. As discussed above, if receivers associate individual males with established social relationships and past interactions (Cheney & Seyfarth 1990), calls' being individually distinctive is potentially at the root of many responses, especially for within-group receivers.

The *boom's* function in facilitating group cohesion is undoubtedly secondary to its role in mate attraction (above), yet females' tendency to approach and maintain proximity with a caller does not appear limited to estrous females. Spending more time close to the male may provide group members with benefits beyond mating (e.g. protection), and thus is sought by estrous and non-estrous females alike. The *boom's* role as a signal of benign intent (i.e. signal content likely includes callers' behavioral commitment / reduced likelihood of aggression after calling) could thus explain a general response of increasing proximity to the caller. Though speculative at this point, it is possible that non-mating group members increase their own access to males by capitalizing on the ability of estrous females (who are more motivated to approach the male) to evoke a *boom* and its assurance of no aggression.

SELECTION FOR SIGNAL DIVERGENCE

In Chapter 1 (pp. 12-17), I described a model for the emergence of novel signals in which selection, acting on variation within existing signals, favors distinctiveness and thus divergence of signals. The inconvenient habit of signals not to fossilize, however, makes definitive conclusions about the evolutionary history of vocal behavior

exceptionally difficult to nail down, though an among-species comparative approach can be extremely informative. The relatively few studies that have examined vocal traits from a phylogenetic perspective have typically done so by comparing the distribution of signals (or features of signals) among extant taxa to species trees derived from morphological or molecular data (e.g. McCracken & Sheldon 1997; Macedonia & Stranger; Lusseau 2003; Cap et al. 2008) or, less commonly, by *combining* vocal traits with molecular or morphological data in phylogenetic analyses (e.g. Gautier et al. 2002). Such studies can shed light on when in evolutionary history certain signals might have emerged, and can provide hypotheses about the relative importance of different signals in regard to, for example, reproductive isolation (e.g. Seddon 2005), social structure (e.g. McComb & Semple 2005), and habitat type (e.g. Slabbekoorn & Smith 2002).

As the present study included only a single species, a temporal evaluation of the emergence of new signals is not possible. By examining variation in acoustic structure among signals in conjunction with variation in function and contextual usage, however, hypotheses about the mechanisms of signal divergence can emerge. In this section, I explore acoustic differences among signals in the vocal repertoire of adult male blue monkeys in light of the functional explanations provided in Chapter 4. This evaluation will refer to three figures (Figs. 1, 2, and 3), each of which contains elements derived, modified, or directly taken from figures appearing in earlier chapters.

Assumptions

The following evaluation of the male vocal repertoire hinges on a few basic assumptions, derived primarily from principles of phylogenetics and cladistics; the

appropriateness of these assumptions is not necessarily substantiated for evaluating within-species variation among signals, yet they present a reasonable place to begin.

1. The vocal signals used by a species constitute a suite of traits that are ***related*** in the sense that they share a common mode of production and principal function (i.e. communication) and thus likely have a common evolutionary history.
2. Vocal signals are ***derived*** from other signals, and thus signals in the repertoire share a common "ancestral" signal structure.
3. Signal divergence follows a bifurcating pattern.
4. Selection favoring distinctiveness among or between signals is the driving evolutionary force of repertoire expansion. Therefore, greater selection pressure is inferred when acoustic distinctiveness is greater.
5. The selection pressure associated with divergence can be inferred from the current function of signals.

    - this last assumption is critical to the evaluation that follows, yet is perhaps the most tenuous. Functional explanations for a signal address *current* selection pressures favoring a behavior (i.e. how signals are maintained). Though possible (and in some cases likely), it is uncertain whether the same factors were associated with a signal's origin.

Acoustic Relatedness (Figs. 1 and 2)

The pattern of acoustic separation among call types (revealed by principal components and hierarchical cluster analyses; Chapter 2) clearly indicates three distinct call structures. The acoustic structure of *ants*, *pyows*, *kas*, and individual units of *katrains* is

similarly configured as a series of 3-4 well-defined energy bands, with the lowest peaking at around 300-350 hz. The *pyow* is typically about twice as long in duration as these other signals, suggesting that a shortening of the *pyow* (or *pyow*-like variant) led to the divergence of the other signals. Though one could argue the opposite (i.e. that lengthening, not shortening, led to divergence), this directionality is supported by the observation that, especially during longer bouts, *pyows* typically become successively shorter and harsher ("*pyowish-ants*") and can sometimes transition fully into bouts of *ants*; the reverse of this (repeated *ants* becoming progressively more *pyow*-like) was never observed.

Ants, *kas*, and the individual units of *katrains* are quite similar in structure, having nearly the same average duration and fundamental frequency. What most distinguishes these calls is the huge difference in energy concentrated at higher frequencies: *ants* have energy distributed evenly up to 3000 hz, with an average center frequency of 1620 hz, whereas *kas* have relatively little energy above 1800 hz and average center frequencies closer to 850 hz. The multi-unit structure of the *katrain* remains a puzzle, as no other male vocal behavior suggests an antecedent.

The *nasal scream* constitutes its own cluster, with a structure quite different from other call types. Unlike *booms*, however, that also cluster far from the other call types, the *nasal scream* comprises distinct energy bands arranged in formants, indicating it shares a basic production mechanism with the other call types; the extreme acoustic variation (i.e. gradedness), especially in terms of duration and center frequency, identifies the *nasal scream* as the least stereotyped and perhaps the least filtered of the male vocalizations.

The acoustic structure of the *boom* is so far removed from that of other call types as to suggest a fundamentally distinct method of production and thus evolutionary history (i.e. it is difficult to imagine that *booms* diverged from any other vocalization). As in several close relatives of blue monkeys (*Cercopithecus nictitans*, *C. campbelli*, *C. neglectus*, *C. mona*, *C. pogonias*, *C. hamlyni*, and *C. lomamiensis*; Gautier, 1988; Hart et al. 2012), *booms* of blue monkeys undoubtedly rely on resonating an inflated laryngeal air sac (Gautier 1971). In laboratory experiments with Debrazza's monkey (*C. neglectus*), Gautier (1971) surgically punctured the air sac of an adult male and then recorded his vocalizations; once recovered, the subject still attempted *booms*, but the signal's amplitude and structure were tremendously diminished, demonstrating the *boom's* complete reliance on the air sac. Production of male blue monkeys' other call types likely also involves the air sac in amplification and lowering the fundamental frequency of the signal (Fitch & Hauser 1995; Hewitt et al. 2002); the acoustic structure, the distinctive "inflating" posture that accompanies them (Chap 2), and the work of Gautier (1971), however, indicate that *booms* are dependent on the air sacs whereas other call types are supplemented by them. The observation that male redtail monkeys (*Cercopithecus ascanius*), a relative of blue monkeys lacking air sacs (Hewitt et al. 2002), use signals remarkably similar to *ants* and *katrains*, yet do not *boom* (Cords & Sarmiento in press; unpublished data) provides additional, albeit indirect, support for this hypothesis.

Signal Function and Acoustic Divergence (Figs. 2 and 3)

When examining related entities, such as species, genes, or vocal signals, it is impossible to observe divergence directly. Divergence is a cumulative process that occurs

over evolutionary time, making any identified "split" between two biological entities less a temporally isolated event than a heuristic description of a continuous process. We can, however, infer the evolutionary distance between two traits – and thus the existence of selection acting upon some ancestral condition – based on their degree of similarity relative to other related traits.

In describing the evolutionary trajectory of behavioral elements, Lieberman (1984) characterized branch points as moments "at which the course of evolution can potentially be changed by virtue of selection for a new mode of behavior that is of value to a group of animals." In the following examination, I use the relative acoustic similarity among call types to infer the existence of such branch points and the functional explanations for call types to infer selection favoring signal divergence.

Vocal Signal "Tree" In Chapter 2, I examined groupings of call samples using an agglomerative hierarchical cluster analysis (i.e. connectivity-based clustering) based on similarity of acoustic features. The results were consistent with the patterns of acoustic distinction among call types described above, and provided quantitative distances among call types and groups of call types. For the current investigation, I employed the dendrogram derived from the aforementioned hierarchical cluster analysis. Dendrograms graphically depict the relative dissimilarity between samples and clusters of samples, with the points at which clusters join referred to as nodes. Here, I considered each node a branch point (*sensu* Lieberman 1984), indicating points at which selection favored divergence among signals. Figure 2 re-presents the dendrogram shown in Chapter 2 (Fig.

3, p. 96), flipped vertically and slightly modified in a not-so-subtle effort to resemble a phylogenetic tree.

To identify selection factors associated with each branch point, I used a method based loosely on traditional cladistic analysis. First, using results for each call type detailed in previous chapters, I treated elements of signal content, patterns of contextual usage, and functional explanations as characters with the states *present* or *absent* (Table 1). I then examined the character states of each call type in relation to those of other call types to determine the efficacy of each character in explaining the bifurcating pattern of signal acoustic structure (i.e. dendrogram, Fig. 2).

Patterns across call types indicated some characters would *not* be useful in explaining signal divergence (Table 1)[1]. If a character state is common to all or among highly diverged call types, it is not likely indicative of selection on divergence; sharing among call types suggests the character state is the "primitive" condition (i.e. symplesiomorphic). Callers' *identity* is an element of signal content in highly diverged calls (*boom*, *pyow*, *katrain*) and its inclusion, though not assessed for every call type, is possibly common across the repertoire. Similarly, some function in both mate defense and group cohesion was identified for the *boom*, *pyow*, and *katrain*, and may relate to other call types. Lastly, as *body size* as content was only assessed for *pyows*, the lack of known character states for so many call types makes *body size* uninformative; similarity in acoustic structure between *pyows*, *ants*, and *kas* suggests this character may be shared with other call types.

[1] It is important to note that suggesting these characters do not constitute primary drivers of signal *divergence* does not in any way discount their adaptive significance to signal *maintenance*.

Excluding the aforementioned characters left eight (Table 1) to potentially explain the divergence among call types. I compared the pattern of character states for call types to the pattern of acoustic dissimilarity among call types and assessed the degree to which differences in character state conformed to the bifurcating pattern of divergence (Fig. 3).

Interpreting the tree The acoustic dissimilarity between the *boom* and all other call types is by far the greatest and, as discussed above, there are reasons to think the *boom* may be fundamentally distinct from all other vocal behavior; considering the *boom* related to or derived from any other male vocalization may therefore be unwarranted. The *boom's* extreme acoustic distinctiveness is, however, still highly consistent with character distinctiveness – its role in affiliative interactions, function in mate attraction, and relative lack of association with disturbances are each unique in the male repertoire. This functional exclusivity indicates that, whether these characters relate to *divergence* between the *boom* and other vocalizations or not, the pairing of functional specificity and acoustic distinctiveness has still been favored by selection.

In addition to the biological reasons not to do so, considering the *boom* part of the diverged signal repertoire also poses one practical challenge to interpreting the bifurcating pattern of the repertoire – the *boom's* inclusion of social status as content, a character state common to all but the *nasal scream*, suggests that status as content is a primitive condition that *nasal screams* lost. If, instead, *booms* are excluded from the evolutionary divergence among signals, the *nasal scream* appears an excellent candidate for "basal" signal, with the inference that *booms* independently evolved social status as content.

All call types other than the *boom* occurred overwhelmingly more with disturbances than non-disturbances. This pattern distinguishes the evolution of *booms* and that of other vocalizations, suggesting that an association with **disturbance contexts** is the primitive state and a conserved character of the other five signals. The first branch point of this cluster divides the *nasal scream* from all other call types, with the inclusion of **social status** as content being the most distinguishing character state (*nasal screams* do not include status as content, whereas all other call types do). The *nasal scream's* use exclusively during intense aggression between males is also unique; though *pyows* are frequently used in male-male agonism as well, enormous qualitative differences distinguish contexts in which the two calls occur (see chapter summaries, above).

The next branch point divides most *pyows* from all other call types. Hierarchical cluster analysis resulted in two distinct clusters of *pyow* samples (in Fig. 3, designated $pyow^1$ and $pyow^2$). These were not discriminated as distinct call types, yet inspection of acoustic features revealed that samples in the secondary cluster (hereafter: $pyows^2$) were typically shorter in duration, harsher (i.e. energy more distributed across frequencies), and exhibited smaller formant dispersion (Chapter 2). It should not escape notice that these same differences, though much amplified, also distinguish *pyows* from *ants*. At the time of this writing, the question of whether $pyows^2$ were significantly more associated with terrestrial predators then $pyows^1$ has not been addressed; field observations and a cursory examination of acoustic data, however, suggest that the shorter, harsher $pyows^2$ were more likely to occur in association with dogs than other contexts. In examining the branching pattern of signal distinction, I therefore treated $pyows^1$ as adhering to the character states described for *pyows* in general and allowed $pyows^2$ to take on an

admittedly vague association with terrestrial predators. This assignment leaves the *pyow*[1] branch distinguished from all other call types as a generalized alert signal (i.e. relatively broad in regard to contextual usage, function, and content), with all the remaining signal types associated specifically with **predators**.

The next branch point along the *Predator* branch divides *pyows*[2] from the cluster comprising *ants*, *kas*, and *katrains*. One convenient interpretation of this pattern relates to the above description of *pyows*[2] as being both associated with terrestrial predators and acoustically intermediate between *pyows* and *ants*. Much more research is required to make conclusions, yet the observation that *pyows*[2] are functionally similar to *ants* yet acoustically intermediate to *ants* and *pyows* is consistent with hypotheses that *pyow*[2] is a transitional form that could constitute, alternatively, a residual of past selection on divergence between *pyows* and *ants*, a redundant recapitulation of past divergence, or current incipient divergence.

The last branch point evaluated is that between *ants* and *kas* / *katrains* (note: in the current evaluation, I treat *kas* and *katrains* as a singular call cluster, an approach justified by the extreme acoustic similarity between *kas* and individual units of *katrains*, as well as the extreme overlap in contextual usage of the two signals; the *katrain's* multi-unit structure, however, makes it unquestionably distinctive and certainly reflects greater divergence than implied by this lumping). The strong acoustic similarity and the common association with predators between *ants* and *kas* / *katrains* supports the hypothesis that these signals are closely related and that presence of predators, perhaps of any class, was the primitive condition. The character state dividing these two signals is unquestionably

the **class of predator**, with selection favoring distinct signals for terrestrial (*ants*) and aerial (*kas* / *katrains*) predators clearly of primary importance to signal divergence.

Evolutionary Divergence of Signals

Integration of results from the various investigations of this study suggests a stepwise path for signal divergence, and an evolutionary trajectory for repertoire expansion in which divergence was driven primarily by selection favoring successively greater contextual specificity. The preceding examination provides a reasonable, inferred model for the expansion of the repertoire of male blue monkeys:

1. The *boom*, though governed by the same functional processes as any other communicative signal, evolved in a separate trajectory, somewhat independent of other call types. It is neither derived from, nor does it share a common vocal "ancestor" with any of the other signals in the male repertoire.
2. The *nasal scream* appears the most primitive (plesiomorphic) of the remaining call types, and thus represents a "basal signal;" the *nasal scream* is likely most similar to an ancestral vocalization that acted as the source from which other signal types diverged.
3. The *pyow* diverged from its common "ancestor" with the *nasal scream*, surely driven by multiple selection pressures favoring greater stereotypy, but primarily by selection favoring a signal that reliably indicated callers' association with a female bonded group (i.e. parallel or subsequent to the emergence of unimale groups and thus resident status).

4. Perhaps relating to residents' increased proximity to mates and offspring (i.e. inclusive fitness), selection favoring reliable predator warning signals drove divergence of *pyows* to form a consistent, though perhaps generalized predator alarm (similar to *pyow*^{2}).
5. Because responses for avoiding terrestrial predators (e.g. move up, mob, look down) differ from those for aerial predators (run down, seek cover), selection then favored splitting this generalized alarm call into the terrestrial specific *ant* and the aerial specific *ka*.
6. The extreme divergence indicated by the *katrain's* multiunit structure is somewhat difficult to explain, though it may simply reflect a relatively higher threat posed by raptors. In flight, birds of prey are above the typical line of sight of most monkeys and are likely to arrive and attack swiftly. The response time suited to avoiding raptors, therefore, is likely quite short relative to that for some terrestrial threats (e.g. snakes, leopards), and the acoustic similarity between *ants* and *kas* may have favored a more dramatically distinct signal.

Directionality Though alternative interpretations of the same data might generate other equally valid hypotheses, there are several reasons to have confidence in the directionality of repertoire expansion described above. If we again set aside the *boom* for a moment (see below), the rest of the male vocal repertoire is consistent with a pattern of repeated bifurcating divergence. The absence of an identified outgroup or any temporal component in this examination precludes a confirmable assignation of character state polarity, yet a little parsimony combined with the right starting point can be quite

informative. The relationship between *ants* and *pyows*[1 + 2] provides such a starting point and perhaps the best evidence of directionality. As discussed above, longer bouts of *pyows* often grade into *ants*, with successively shorter and harsher *pyows* giving way to proper *ants*; the reverse (repeated *ants* becoming progressively more *pyow*-like) was never observed. Furthermore, relatively shorter, harsher signals may reflect reflexive constriction of muscles in the vocal tract relating to higher arousal states (Morton & Wiley; Fitch & Hauser 1995), consistent with a *pyow*-like signal associated with general arousal being transformed by higher arousal associated with predators.

Accepting that *pyows* "begat" *ants* anchors the directionality of divergence inferred for the rest of the repertoire. *Kas* could thus not have begat *ants*, but rather must have diverged from them or a common *pyow*[2] -like signal. The biggest structural difference between *ants* and *kas* is the *ka's* relative lack of energy above 1800 hz, suggesting that, mechanistically, vocal tract filtering of energy at higher frequencies drove divergence between *ants* and *kas* (Fitch & Hauser 1995).

The pattern of directional divergence favoring shorter calls with greater contextual specificity is consistent for *pyows* through *kas*, leaving the *nasal scream*, by default, in the basal position. Beyond the process of elimination, however, there are other reasons to consider the *nasal scream* primitive to other call types. It is by far the most acoustically variable of the repertoire and exhibits energy distributed widely across the frequency spectrum; this indicates a deep well of variation on which selection could act, and that application of frequency filters and shortening of duration could produce several novel signal types from this one basic structure. That it is shared by all adult male social classes and bears strong acoustic similarities to calls in the adult female and juvenile repertoires

(discussed in Chapter 2) likewise supports its ancestral position. Puzzlingly, though the pattern from *pyows* to *kas* suggests the most primitive signal should have the least functional specificity, *nasal screams* actually exhibited some of the highest contextual specificity (i.e. associated with male-male aggression only). Though perhaps best left a puzzle, one might speculate that the ancestral signal, a highly graded *nasal scream*-like vocalization, was used quite generally and reflected varying states of arousal in callers; as selection favoring more contextual and functional specificity led to emergence of different call types, the *nasal scream's* singular role in intense aggression may have resulted simply from the signal's loss of other functions, rather than selection favoring its specificity.

The *boom* challenges this otherwise neatly summarized evolutionary hypothesis for blue monkey vocal signals. The *boom* is an internally produced acoustic signal with a pattern of usage and receiver response unquestionably in keeping with those of other vocal signals. Like for other call types, selection has also clearly favored the pairing of *booms'* acoustic distinctiveness with specificity of function and content. The *boom's* resemblance to other signal types in terms of acoustic structure, however, is so faint that a shared evolutionary history is difficult to imagine. In the other call types, it appears that selection favored acoustic divergence to capitalize on benefits relating to function and content, whereas this direction may be reversed for *booms* (i.e. selection may have favored mapping important elements of function and content onto an acoustically unique signal that emerged via a very different evolutionary path).

In the absence of among-species comparison or any real or inferred temporal component, any conclusions about signal evolution based on the preceding evaluation are

speculative. The picture emerging from an integrative exploration of this study's results does, however, present a logically derived hypothesis for both the manner and mechanism of signal divergence – a hypothesis that provides insight into blue monkey vocal behavior and, most importantly, can serve as foundation to future studies that attempt to confirm or falsify it.

FUTURE DIRECTIONS

Despite centuries of study, numerous discoveries, and important advances in both theoretical and applied research, our understanding of how animals communicate remains something of a patchwork, with questions continuing to far outpace answers. The research presented in this dissertation adds to this mosaic, hopefully by answering questions of merit but, most importantly, by providing a foundation for continued exploration. The presented quantitative analysis of acoustic structures, identified elements of signal content, and systematically derived functional explanations constitutes an objective description of call types that is relevant to future examination of blue monkey behavior as well as comparative analyses across taxa.

The possible avenues for expanding upon the research begun here are practically infinite. In addition to refining some of the functional and mechanistic conclusions of the current investigation (e.g. examine other potential elements of signal content), several areas of study are likely to be especially generative; here, I suggest a few.

Within-Species Studies The high degree of sexual dimorphism in the blue monkey vocal repertoire undoubtedly reflects sexual selection on the physiology and behavior of adults (Andersson 1994). It remains unclear, however, when developmentally and in what manner male and female repertoires diverge. Not surprisingly, the structures of vocal signals of many primates change as animals age (e.g. marmosets, Pistorio et al. 2006; capuchins, Gros-Louis et al. 2008), and these changes are often more pronounced between the sexes, especially as they approach maturity (reviewed in Ey et al. 2007). In most studies, however, sex- and age-related differences have been examined in signals where the basic acoustic structure is fundamentally the same (i.e. within call type), with variation seeming primarily to reflect differences in body size (Ey et al. 2007). In blue monkeys (and several other *Cercopithecus* species; Gautier 1971), the adult male vocal repertoire is completely distinct from that of other age-sex classes, and appears to emerge quite suddenly at sexual maturity. The vocal repertoires of juvenile blue monkeys of both sexes appear extremely similar to that of adult females (unpublished data), suggesting that dramatic changes – physiological, social, behavioral, or some combination of the three – associated with adulthood contribute to transforming the vocal repertoire of males. Future research should examine the ontogeny of vocal behavior of blue monkeys, characterizing differences in usage and acoustic structure of signals of all age-sex classes. Once a quantitative description of the acoustic repertoire for the entire species is available, it will also be possible to determine whether the repertoire of adult males is truly distinct, or if some signals reflect extreme modifications of structures seen in the female repertoire (e.g. is the *pyow* a uniquely male signal, or "simply" an amplified version of a *chirp*).

Among-Species Studies Across taxa, an ever-growing number of studies of vocal behavior provides opportunity for comparative analyses that can improve understanding of how communication systems evolve. Some researchers have explored the utility of vocal signals as characters for reconstructing phylogenies and found strong agreement with phylogenies derived from morphological and molecular data (e.g. birds, McCracken & Sheldon 1997; cercopithecine primates, Gautier 1988, Gautier et al. 2002; deer, Cap et al. 2008). In these and similar studies, however, types or features of signals are treated as character states, limiting analyses to distinctions based on presence-absence. With modern spectrographic techniques and multivariate analyses, there is also opportunity for comparing vocal signals of different species in terms of multidimensional, continuous variation. For example, using acoustic data for vocalizations across species in hierarchical cluster analyses (as described in Chapter 2) could illuminate the degree to which *variations* of different call types are shared across taxa, and how much they change in conjunction with species' divergence. Such an exploration would reduce the subjectivity inherent in identifying "analogous" call types or features, and could also shed light on why some acoustic structures appear conserved across related taxa, whereas others are apt to be lost in speciation. For example, calls by male blue monkeys bear strong resemblance to calls described for some congeners, though the link between "call-sharing" and phylogenetic relatedness (using Disotell & Raum 2002) is unclear: male putty-nosed monkeys (*C. nictitans*), the nearest congener of *C. mitis*, produce *booms* and *pyows* similar to those of blue monkeys, and *hacks* similar to *kas* (see Fig. 1 in Price et al. 2008; Gautier & Gautier-Hion, 1977; Gautier, 1988), but do not appear to share the multi-unit *katrain*; though reflecting similar genetic distance from blue monkeys,

DeBrazzas monkeys (*C. neglectus*) produce *booms* whereas (*C. ascanius*) do not; furthermore, redtail monkeys use signals similar to blue monkey *ants* and *katrains*, yet do not *pyow* or *boom* (unpublished data; Cords & Sarmiento in press). Additionally, understanding of signal evolution can be improved by among-species examination of how acoustically similar signals may differ in function and, conversely, how acoustically dissimilar signals may achieve similar functions.

Hybrid Studies Studies of hybrid offspring can provide unique insight into the relative contributions of genotype, ontogeny, and social learning on animal behavior. For vocal behavior in particular, such examination may also illuminate the degree to which signals function in species recognition, mate choice, and reproductive isolation (e.g. Saetre et al. 1997) and may thus contribute to understanding patterns of speciation. Where it has been examined, the vocal behavior of hybrid offspring often appears to be acoustically intermediate relative to parental species (e.g. deer, Long et al. 1998; seals, Page et al. 2001; quails, Derégnaucourt 2010), likely indicating genetic determinism for vocal behavior and admixture of genes relating to signals. Labeling signals "intermediate" is, however, a quantitative assessment, and the biological significance of differences in hybrid vocal behavior remains poorly understood.

Recent observations of hybrids between *C. mitis* and redtail monkeys (Detwiler 2002) and vervet monkeys (De Jong & Butynski 2010) provide promising opportunities to investigate the evolution of primate vocal signals. In both these cases, adult male hybrids vocalized, though the degree to which the hybrid signals adhere to signal structures described for either parent species has not been evaluated. The authors suggest, however,

that the signals of hybrids of both crossings are more consistent with those of *C. mitis* – adult male redtail hybrids produced *pyows* (K. Detwiler, pers. comm.) and a vervet hybrid produced *pyows*, *katrains*, and *booms* (De Jong & Butynski 2010). The occurrence of *booms* in the vervet hybrid is especially interesting, as vervet monkeys lack the air sacs (Hewitt et al. 2002) essential to producing this signal (Gautier 1971). In addition to expanding understanding of signal divergence, examining the vocal behavior of these hybrids may help elucidate patterns of allele dominance, and the role of male vocal signals in mating behavior.

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Table 1. Character states for each signal, based on investigations of content and function. For each call type, '**+**' indicates character presence and '**-**' indicates absence; cell marked "±' indicates evidence was equivocal but tended toward presence. Cells marked '**?**' indicate data were insufficient to determine character state. Shaded characters were excluded from subsequent analyses due to lack of explanatory value (see text).

	CHARACTER	BOOM	NASAL SCREAM	PYOW	ANT	KA	KATRAIN
Signal Content	Identity	+	?	+	?	?	+
	Body Size	?	?	+	?	?	?
	Social Status	+	-	+	+	+	+
Contextual Usage	Intense Aggression	-	+	-	-	-	-
	Disturbance	-	+	+	+	+	+
	Affiliative Interaction	+	-	-	-	-	-
	Non-Disturbance	+	-	-	-	-	-
Function	Mate Attraction	+	-	-	-	-	-
	Predator Alert (terrestrial)	-	-	±	+	-	-
	Predator Alert (aerial)	-	-	-	-	+	+
	Group Cohesion	+	-	+	?	?	+
	Mate Defense	+	?	+	?	?	+

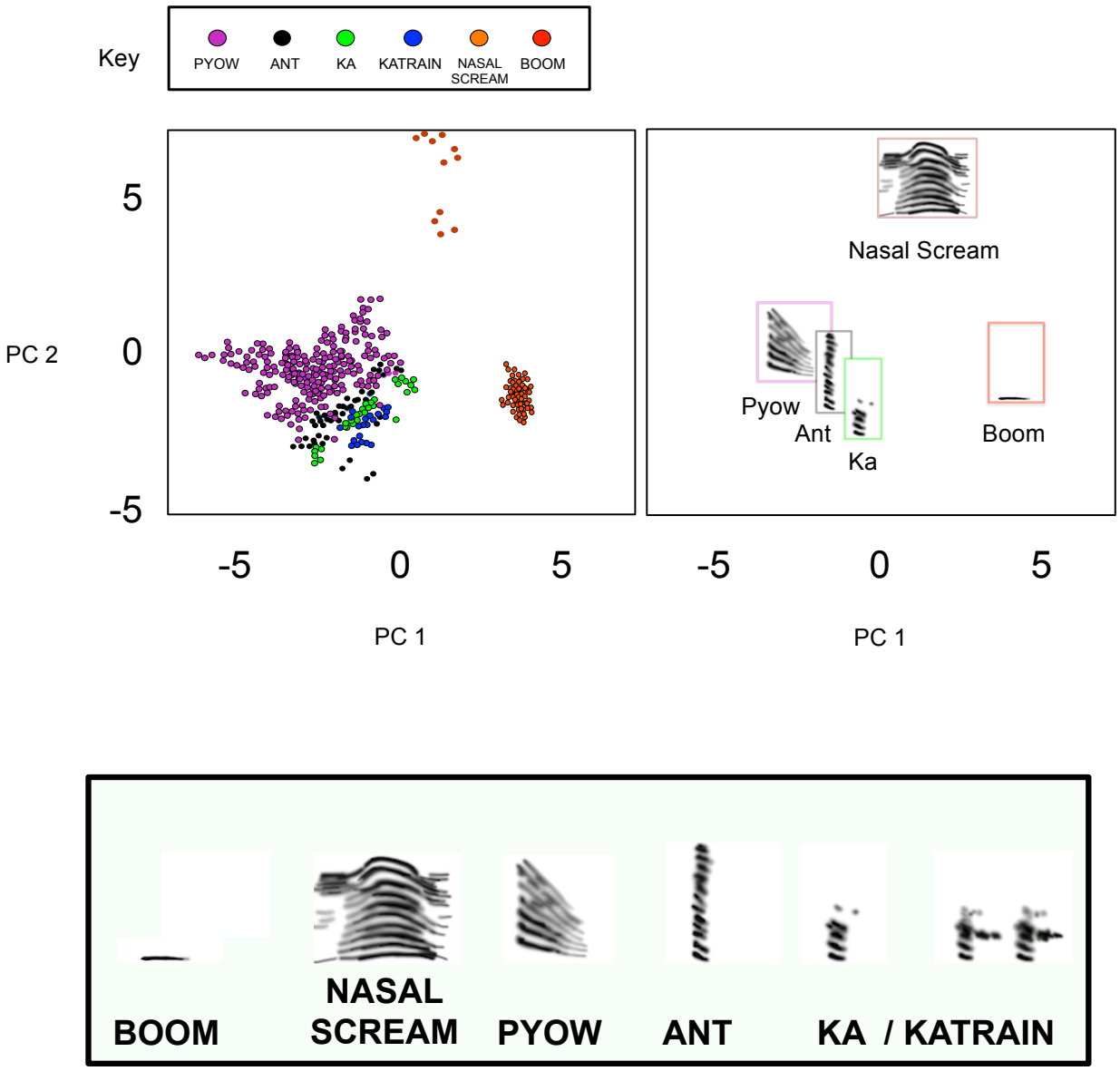

Figure 1. The acoustic structure of the male vocal repertoire. The bottom panel shows exemplar spectrographs of each of the six call types (see Chapter 2 for detailed description of acoustic structure). Above, call samples are shown plotted in space defined by principal components (left), with the same information repeated with exemplar spectrograms substituted for call sample points (right).

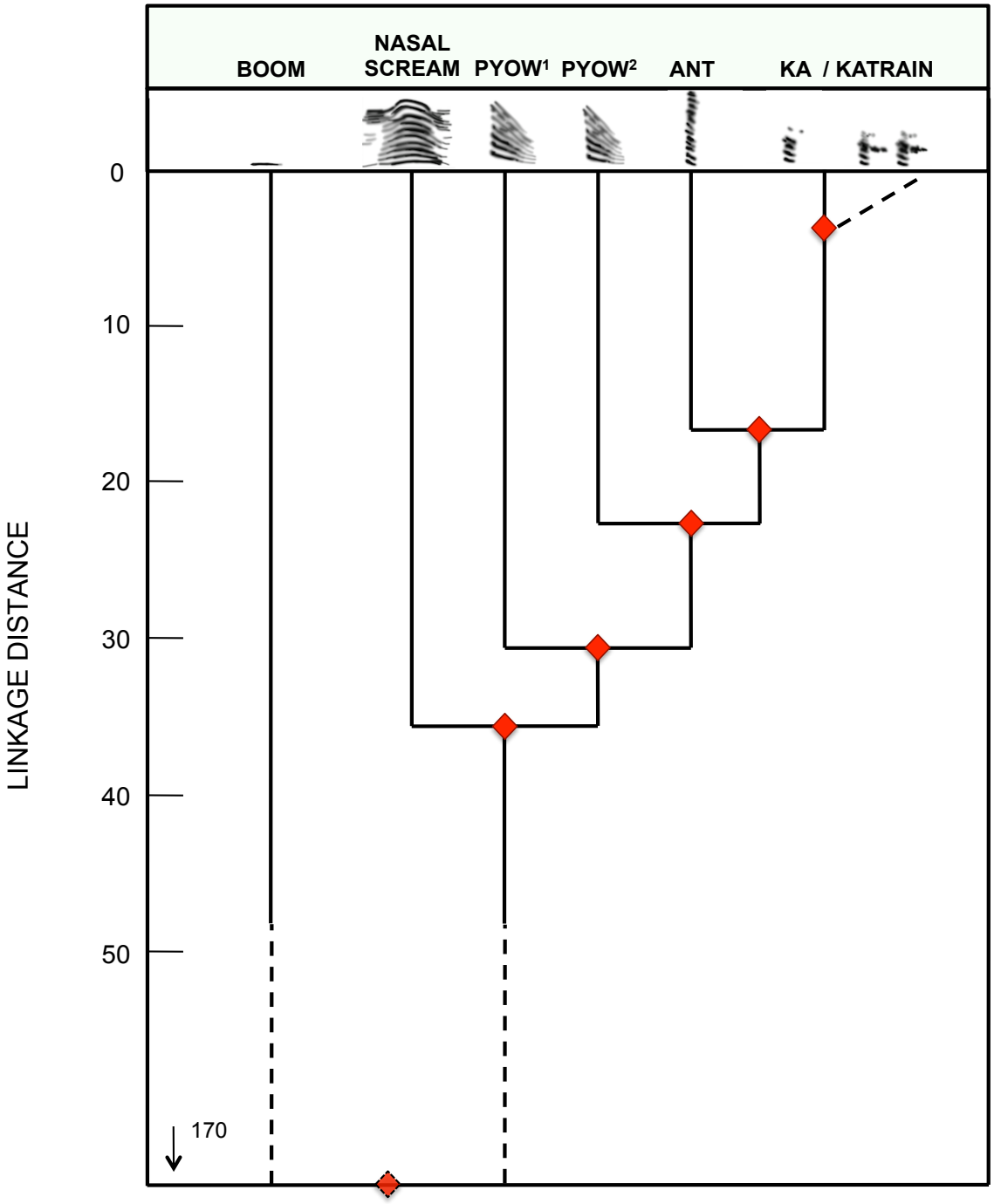

Figure 2. Dendrogram derived from hierarchical cluster analysis of call samples based on acoustic features (details in Chap 2). Vertical lines show distances between clusters of samples, horizontal lines show where groups joined. Red diamonds placed at nodes represent inferred evolutionary branch points between signal types. The point for the multi-unit *katrain* is speculative, and does not reflect quantified distinction between it and other calls. *Pyows*$^{(1+2)}$ clustered separately, yet were not discriminated as distinct call types by DFA; *pyow*^{2} samples tended to be shorter and with smaller formant dispersion.

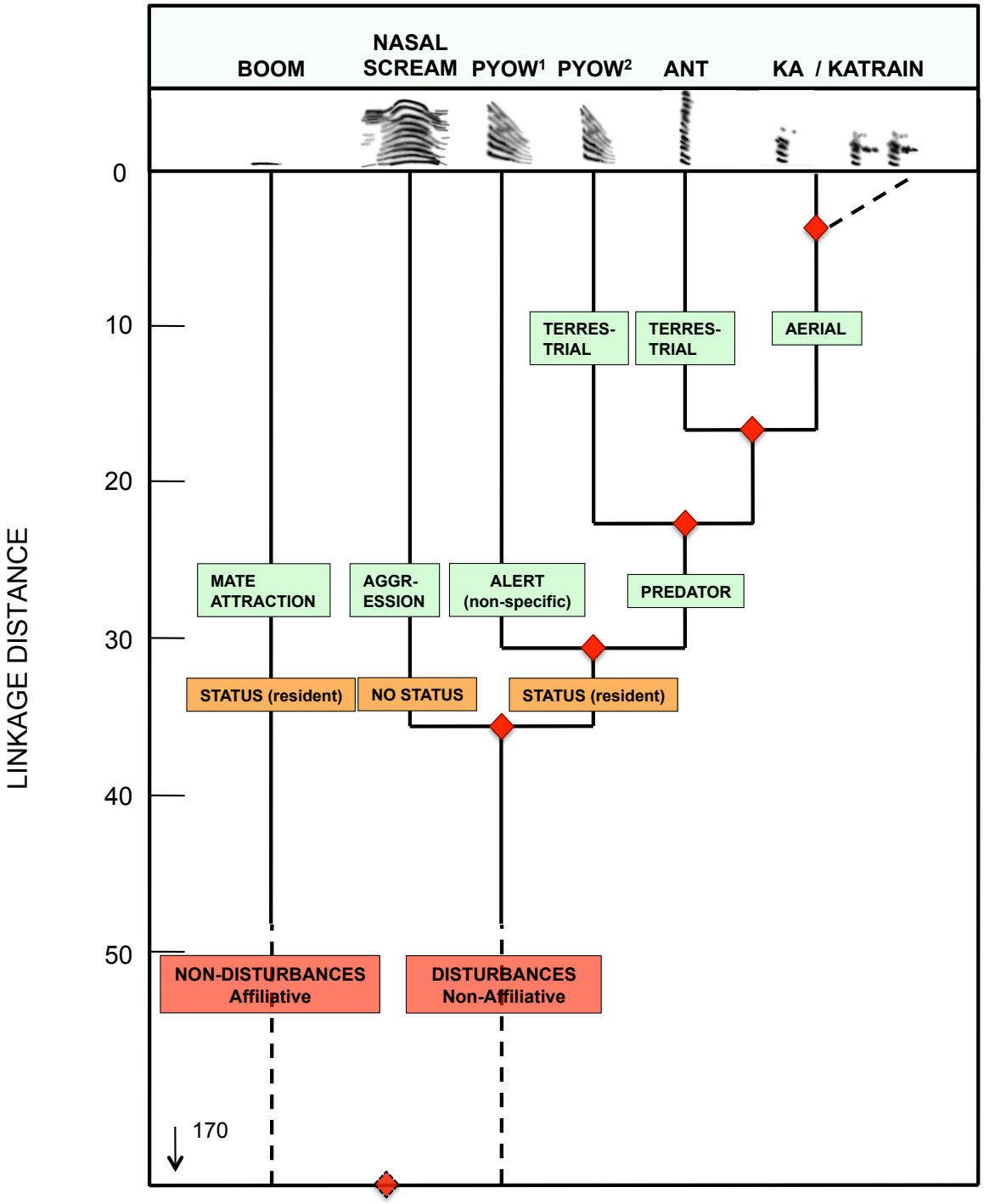

Figure 3. The same dendrogram described in Figure 2. Text boxes refer to character states based on signals' patterns of contextual usage (red), content (orange), or function (green). Boxes are placed on branches according to character states that are unique to the call type or group of call types beneath them (with the *boom's* inclusion of social status the exception). Each call type, therefore, reflects nested and successively more specific character states.